SOME OBSERVATIONS ON THE DIGESTIVE SYSTEM OF DIPLOPODS WITH SPECIAL REFERENCE TO PARAJULUS.

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By

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I. INTRODUCTION.

The present paper is primarily a comparative gross anatomical and histological study of the digestive tube and associated glandular appendages in four American genera of Diplopods; Parajulus (Humb. and Sauss.), Scytonotus (Koch), Orthomorpha (Boll.) and Fontaria (Grey). None of these forms have been touched upon regarding their digestive system in any previous works, though Parajulus and Fontaria have been incidentally referred to by Crawley (1903) as the hosts of a number of midintestinal Gregarine parasites. Inasmuch as the literature dealing with this relatively unpopular field of investigation is to a large degree widely scattered and fragmentary, I have been especially concerned with bringing it together in such a form that my own contributions may be clearly correlated at every point with observations already made on other genera. To a more limited extent I have included insects and other Arthropods within the range of my comparisons and have, perhaps, diviated somewhat from the general trend of my paper in recounting the results of some starvation and hibernation experiments on the midintestinal epithelium of Parajulus. While in many instances my observations are inconclusive and merely affirm or deny previously established interpretations, I am assured that in others new increments have been added to our present knowledge of the digestive tracts of Diplopods.

Morphologie und Entwickelungsgeschichte der Chilognathen", published in 1877. In 1878, as a supplement to his monumental work on the digestive process in insects of 1874, appeared Plateau's,"Recherches sur les phenomenes de la digestion et sur la structure de l'appareil digestif chez les Myriapodes de Belgique", which was a considerable advance beyond all previous attempts in this direction. His results are based on three species of Julus not touched upon by earlier authors; J.Londinensis (Leach), J. sabulosus (Linn.) and J,terrestris (Linn), and on the two species of Glomeris described by Brandt, G.marginata(Leach) and G.limbata (Latreille). Although he made no sections and therefore missed a great many of the finer histological details, he was the first to accurately describe the course of the tubular glands in Julus and Glomeris and, in so far as I can determine, the only one who has carefully studied the food content of the alimentary canals of Diplopods and analysed the secretions of the midgut and tubular glands. The next reference to the digestive tract of Diplopods comes from vom Rath whose, "Zur Biologie der Diplopoden", of 1890 notes that polydesmids undergo a complete renewal of the midintestinal epithelium during moults, and whose "Beiträge zur Kenntnis der Chilognathen", published the following year, describes the midintestinal cells of Polyxenus lagurus (de Geer) as being especially large and provided with ameboid processes. Heathcote, in 1890 published a very brief paper, " On some points of the anatomy of Polyxenus lagurus (De Geer)", which accurately but incompletely describes the Malpighian tubules and figures them histologically. Then Visart (1895) called attention for the first time to the peritrophic membrane and regenerative cells in his "Contribuzione allo studio del sistema degerente degli Artropodi. Sull' intima struttura del tubo digerente dei Miriapodi (Chilognati),

in which he considers five species of Diplopods; Julus, Tropisoma, Polydesmus, Lysiopetalum and Glomeris together with Orthoptera and Lepidoptera. In a short article of 1902, "Sull' apparecchio digerente dell' Julus communis", Rossi described the duct and opening of the tubular gland which Plateau had overlooked and also limited the number of Malpighian tubules to two instead of four which was previously regarded as the correct number in Julus. During the same year, Silvestri presented a paper, "Sulle ghiandole cefaliche o anteriori del Pachyiulus communis (Savi) which, according to the concensus of subsequent opinion, successfully demonstrated that two masses of tissue, (one situated in the head cephalad of the brain, and the other investing the oesophagus dorsally and laterally in the anterior region of the trunk) are in reality glands rather than fat bodies as had been previously supposed by Rossi, Visart, Plateau and others. This was followed in 1903 by an article of Bruntz, "Sur la présence de reins labiaux et d' un organe phagocytaire chez les Diplopodes", which attempted to prove as a result of injections of ammonium and indigo carmine into the body cavity, that the tubular glands, together with a pair of anteriorly situated alveolated structures, of Julus and Glomeris are anatomically and physiologically interrelated and constitute a labyrinth and sacculus with an excretory function, both of which points are sharply at variance with Silvestri's previous conclusions. That same year, Silvestri completed his "Classis Diplopoda", which forms part of the series, " Acari, Myriapoda et Scorpiones, huiusque in Italia reperta" that he compiled in collaboration with Berlese. This work consists of a very thorough comparative study of the segmentation and appendages of all the ten orders of Diplopods now recognized, together with a detailed account of the embryology and muscular

system based largely on Pachyiulus communis (Savi). I mention it in this connection, because it treats of a number of skeletal structures associated with the pharynx which apparently remained undescribed up to that time. In 1904, Bruntz published his very extensive work,"Contribution a l'etude de l'excretion chez les Arthropodes", and reaffirmed his former views regarding tubular glands of Julus and Glomeris. Here he claims to have obtained almost identical results from five species of Diplopods: Glomeris marginata (Leach), Glomeris guttata (Risso), Julus fallax (Meinert) Julus sabulosus (Linn) and Polydesmus complanatus (Linn), but presents a detailed description and figures of Glomeris alone. Next, Krug, in 1907 furnished a brief but comprehensive treatment of the entire digestive tract in his "Beträge zur Anatomie der Gattung Julus", which was based on his observations of Julus Mediterraneus. From a purely morpholcgical stand point, the work surpasses all previous attempts in as much as it gives us the general histological features of the entire digestive system in this species. As regards the two pairs of salivary glands, anterior and posterior, identified by Silvestri in Pachyiulus, Krug corroborates the latter's view in Julus and finds that their pharyngeal openings are essentially the same, the anterior, dorso-lateral and the posterior, ventro-lateral. He also upholds Plateau's and Rossi's observations on the structure and openings of the tubular glands, but notes three divisions to the hind intestine besides the anal part, rather than the two which Plateau recognized. In the midgut, Krug found a uniform layer of rounded cells peripheral to the muscularis which he suggests may be glandular in function as opposed to Visart's contention that they are fat cells. He contents himself, however, with describing the gastric epithelium as a simple layer of cylin-

drical cells and denies the existence of a cuticula or intima of any sort. The following year, 1908, Bruntz again came forth with his labial kidney hypothesis, and in a short but firey paper, "Les reins labiaux des Iules", rather sharply rebukes Krug for adopting Plateau's and Silvestri's interpretation of the tubular gland as salivary in function and disregarding his own previous works of 1903 and '04. He furthermore contends that what Krug affirms to be the ducts of the posterior salivary glands are merely apodemes which support the sacculi of the labial kidneys and attach them to the pharynx. As I shall show later on, there is little doubt that Bruntz simply confused Krug's description of the posterior salivary glands with his own observations on the sacculus and that the former was completely overlooked by Bruntz and the latter by Krug. In 1909, Effenberger presented a paper on Polydesmus complanatus (Linn.) which he treats in very much the same way that Krug treated Julus. He found the anterior and posterior glands to be very similar to those of the latter but was unable to make out their ducts in much detail, but he recognized the tubular glands as branched rather than singly coiled tubes doubled on themselves, and noted a pair of large, dorso-lateral spinning glands in the female opening into the anal part of the hindintestine by means of a pair of very small ducts. He also found that the peripheral layer of cells surrounding the midintestine was lacking in the form. During the succeeding year appeared two more papers of a similar nature; one by Wernitzsch on Craspedosoma simile, and the other by Reinecke on Polyxenus lagurus. Of these, Wernitzsch finds in Craspedosoma, a very close similarity to Julus. The tubular glands are of the same plan of structure but distinctly shorter and thicker, and with the blind terminal ends considerably dilated and showing an epith-

elial structure different from the remaining parts of the gland. Also the midgut is very similar to that of Julus, but he considers the outer cellular layer as hepatic rather than glandular in function. He further noted a pair of small anal glands in both sexes which he looks upon as homologous with the spinning glands of Polydesmus. Reinecke's paper on Polyxenus lagurus describes the anterior and posterior salivary glands very much as represented in the foregoing species, but the tubular gland he shows as quite short and confined to the cephalic region and thus contradicts Heathcote's statement that it extends a considerable distance posteriorly. He found no uniform cellular layer enveloping the entire midgut, but discovered a pair of grape-like thoracic glands supplanting the former laterally and anteriorly. Although he identified ducts leading from them, he was unable to determine where they opened. Reinecke describes very clearly and fully the somewhat unique distribution of the urinary tubules in this form, and in so doing, appears to be the only one who has particularly touched upon this point in Diplopods. Then in 1911, appeared Issajew's paper,"Zur Anatomie des Polyxenus lucidus". Like Heathcote, he refers to the tubular glands as extending far posteriorly, and notes the thoracic glandular mass which he regards as essentially similar to what has already been termed the anterior and posterior salivary glands. He also finds that, in the region of the seventh segment, the midgut is divided by a circular constriction into anterior and posterior parts. A year later appeared a work by Verhoeff entitled "Die Diplopoden Deutschlands" which, from what I can gather, more closely approaches a complete monograph on Diplopoda than anything heretofore published. To this, unfortunately, I have been unable to gain access, but in a paper of 1914, "Die Verwandlungen des Mitteldarmes

von Polydesmus während der Hautungsperioden", Verhoeff states that in the former work, he gives a complete resume of all that has been done on the digestive tract of Diplopods, together with his own observations on the behavior of the midintestinal epithelium of the Julidae thruout the moulting process. During the ecdysis between the 18th and 19th segment instars, he finds that the midintestine of Polydesmus monticclus undergoes almost identically the same processes as in the Julidae, upon which, however, his data are more limited than on the former. In as much as my own observations apparently have no bearing on ecdysis, a brief statement of Verhoeff's most important conclusions will not be out of place here since there will be little occasion for referring to the topic later on.

1. There is a complete epithelial regeneration of the midgut, commencing presumably at the anterior end and proceeding posteriorly.

2. At the bases of the old epithelial cells are many leucocytes which, in the posterior part of the midgut, become very thick and form a ring between new cells on the outside and the old ones on the inside.

3. This ring or leucocytome consists of an outer white body which disappears before the new epithelium is completely developed and from which leucocytes can break away to phagocytise old epithelial remains in the anterior part of the midgut; and an inner yellow body which persists for some time after the former has disappeared and is eventually passed on into the hindgut.

4. The leucocytome with white body included completely plugs the passage from mid to hindgut; but is eventually fragmented and pushed backward by pieces of its own exuvium which the animal has swallowed.

5. The exuvia, all of which is eventually consumed, serves also as a means for providing calcium carbonate to reenforce the chitin of the new exoskeleton.

6. By phagocytosis, the leucocytes act as checks on Gregarine parasites which tend to become very abundant during ecdysis.

7. Verhoeff is not very clear as regards the relationship between the germinal cells of the epithelium and the leucocytes scattered about in the basal region of the epithelium; and he presents no figures showing the changes described in histological detail.

Since 1914 there have apparently been no further increments to our knowledge of the digestive system in this class, but before concluding this summary, I must refer to a paper of Léger et Duboscq, "Nouvelles recherches sur les Gregarines et l'epithelium intestinal des Tracheates", which, though primarily a systemmatic parasitological work describing twelve species of Gregarines all belonging to the single genus, Stenophora, presents also an excellent description of the midguts of Julus albipes C.K., Craspedosoma Rawlinsii simile, Verh. and Polyxenus lagurus (De Geer), together with three figures which, in Julus and Craspedosoma indicate a very close histological similarity to Parajulus and regarding which I will have more to say later on. His figure of Polyxenus shows the epithelium during ecdysis in which the old, cast off cells still cling together in the form of irregular strands and what is especially interesting from a parasitological standpoint, the Gregarine which infest this Diplopod, Stenophora polyxeni , remains intracellular within this tissue and has never been found free in the lumen. The previous year Crawley found a Polycystid Gregarine, Stenophora Julipusilli in a number of American species of Julus

and Parajulus, and I have good reason for believing a Gregarine which I have commonly found in the midgut of Parajulus venustus to be of this species. He also mentions another species from Fontaria which I have failed to recognize in Fontaria virginiensis brunnea. Crawley has nothing at all to say about the digestive tract of the hosts and was unable to identify the species in which he found the Gregarines.

It will be seen from the foregoing that, aside from many which have been recognized as hosts of parasites, seventeen species representing eight genera of Diplopods have been considered from the standpoint of the digestive system and that of these, Julus terrestris and Mediterraneus, Glomeris marginata, Polyxenus lagurus, Polydesmus complanatus, Pachyiulus communis and Craspedosome simile, have received the greatest amount of attention. Of the four genera to be shortly considered, Parajulus belongs to the same order as Julus and Pachyiulus, while Fontaria, Orthomorpha and Scytonotus are all closely allied to Polydesmus, and it is important that this should be borne in mind thruout the following pages.

IV. THE DIGESTIVE TUBE.

1. General Considerations.

As in all Diplopods so far described, with the exception of Glomeris and other Oniscomorphs, the digestive tract of the four species under consideration has the form of a straight tube with a length corresponding very closely to that of the body. In all, the three fundamental regions, foregut, midgut and hindgut are clearly marked. The first readily lends itself to a subdivision into pharynx and oesophagus and the last into intestine and rectum, while the midgut is practically homogeneous from beginning to end. It will therefore be both logical and convenient in the following pages to treat the digestive tube under the three primary headings of foregut, midgut and hindgut and to consider the first under the subheadings, pharynx and oesophagus, and the last under intestine and rectum.

The average dimensions of these regions are shown for the adults of the species in the accompanying tables and in Figures 1-2-3-4. In both sexes as well as in all the immature stages examined they were found to be proportionately the same.

1. Length.

	Pharynx	Oesophagus	Midgut	Intestine	Rectum	Total
Parajulus	0.8-1mm	5-6mm	27-32mm	5-6mm	0.8-1mm	38.6-46mm
Scytonotus	0.6 "	1.6 "	9 "	3.4 "	0.6 "	15.2 "
Orthomorpha	0.7 "	1.7 "	9 "	5.3 "	0.7 "	17.4 "
Fontaria	1.5 "	3.5 "	22 "	16.5 "	1.5 "	45 "

2. Average Diameter.

	Pharynx (Anterior width)	Oesophagus	Midgut	Intestine	Rectum
Parajulus	0.8-1mm	0.2-0.25mm	0.8-1.5mm	0.5-0.8mm	0.6-0.7mm
Scytonotus	0.6 "	0.15"	0.9 "	0.35-0.8"	0.4 "
Orthomorpha	0.7 "	0.16"	0.9 "	0.35-0.8"	0.4 "
Fontaria	1.5 "	0.5 "	1.5-4 "	1-3.5 "	1.5 "

It will be noted that in Parajulus there is a markedly greater variation in size than in the other genera. This not only applies to the sex, the females being distinctly larger than the males, but also to different individuals within each sex. The most important point, however, which the tables bring out is the relative prominence of the midgut as compared with the remaining regions. In Parajulus it comprises over two thirds the entire length of the tract, in Scytonotus three fifths, in Orthomorpha slightly more than one half and in Fontaria slightly less than one half. According to Plateau (1878), Krug (1907) and Wernitzsch (1910), Julus and Craspedosoma come closest to Parajulus in this regard, while the observations of Effenberger (1909), Brandt (1837) and Plateau would place Polydesmus and Glomeris between Scyonotus and Orthomorpha. In Glomeris, the digestive tube takes the form of a single loop, but when straightened out, as Plateau remarks, it shows no special features. Inasmuch as Parajulus, Julus and Craspedosoma belong to the elongated tyle of Chilognath in which the body segments are cylindrical and always more than twenty in number, while the others are short, flattened forms, it is possible to recognize a correlation between the relative length of the midgut and the

body form within the order, Chilognatha. It would be inadvisable, however, to apply this generalization to the Diplopoda as a whole, since the short, 10- segmented Polyxenus, according to Bode (1877) and Reinecke (1910), has a midgut at least two thirds the length of the entire digestive tract.

The positions of the regions of the digestive tube in relation to the segments is dependable only to a slight degree upon muscular contraction and expansion, and may therefore be defined with exactness. In all the Diplopods investigated in this regard, the pharynx is confined to the head and never extends posterior to the brain and oesophageal connectives. The oesophagus ends in the seventh, rarely in the sixth or eighth trunk segment in Parjulus, and in the fourth in Scytonotus, Orthomorpha and Fontaria. The latter agrees with what Effenberger has noted for Polydesmus. In Craspedosoma (Wernitzsch) it ends in the fifth segment, in Julus (Krug) in the sixth, while in Polyxenus (Reinecke) it is confined exclusively to the head. The midgut of adult, 54- segmented Parajuli ends in the fortieth or forty first segment, and in the eleventh or twelfth segments of adult, 20- segmented Orthomorphae and Fontariae, while in Scytonotus with only nineteen segments in the adult stage, it ends in the twelfth. As regards the other genera cited above, it reaches the twenty second segment in the adult, 30- segmented Craspedosoma, the thirty ninth in 49- segmented Juli, the eleventh in 20- segmented Polydesmi and the seventh in 10- segmented Polyxeni. The rectum is always limited to the last or anal segment. (See Figs. 1-2-3-4)

2. Foregut

A. Pharynx.

It would appear that Silvestri (1903) is the first and only investigator who has studied the pharynx of Diplopods in detail and his description, based primarily on Pachyiulus Communis (Savi) but referring to Diplopoda as a class, is applicable in its main points to the genera here considered. Krug, Effenberger, Reinecke and Wernitzsch figure it but refer to it only in the most general terms.

The pharynx is roughly trapezoidal in shape and as wide dorso- cephalad as it is long. With the mouth parts adducted its dorso-ventral diameter, proportionately greater in Parajulus than the others, is nearly uniform for most of its length. Its dorsal width gradually decreases caudad and abruptly narrows at its posterior end where the oesophagus commences, thus forming a rather sharp dorso- lateral angle. (See figures 8A and 9). Ventro-caudad it is narrower than dorso-caudad and posteriorly its ventral wall bends upward at quite a sharp angle, thereby giving rise to a distinct pocket below the opening of the oesophagus. Laterally the pharynx is bounded by the premandibles which, when adducted, completely divide the anterior pharyngeal lumen into upper and lower halves. These structures, homologous with the mandibles of other Arthropods, have been so thoroughly described by Silvestri (1903) and others in Parajulus and the Polydesmoids that I shall touch upon them here only insofar as they are directly related to the pharynx. (See Figures 5, 6 and 7)

(a) Skeletal Structure.

The pharynx is lined by an intima which is a direct continuation of the primary chitin of the exoskeleton, as is clearly shown in my haemalum-eosin preparations, and which is uniformly thickest dorsally and ventrally. Laterally, both above and below the premandibles, it becomes perceptibly thinner but is continuous with the posterior, internal surface of the premandibular molae which is heavily reinforced by secondary chitin and forms the masticatory plate or lamina tritoria (Latzel-1880). In Parajulus, Scytonotus and Orthomorpha, the masticatory plates are smooth but corrugated in Fontaria, while in all four they are penetrated by numerous pores, especially distinct in Parajulus and probably sensory in function. (See Figures 8A, B and 9).

On the dorsal wall of the pharynx, the intima takes the form of three well defined plates, two lateral and one medial, which Silvestri (1903) has named, right and left anterior laminae and median anterior laminette. The laminette is divided from the lamina on each side by a sharp but slight infolding of the intima which becomes less pronounced caudad and disappears entirely at the posterior end of the pharynx. Along its well rounded anterior margins, each lamina presents a distinct row of spines which increase in size medially and culminate in a very large one at each side of the anterior margin of the laminette. Extending caudad from each of the latter along each infolding between lamina and laminette, is a row of large spines flanked laterally and medially by smaller ones, both of which disappear posteriorly together with the infolding itself. At

the anterior margin of the laminette, between the two large spines just mentioned, there is a very pronounced thickening of the intima which takes the form of a ventrally projecting, blunt tooth and, posterior to this, a gradually receding pad which is laterally setaceous but medially comprises a dense mass of fungiform structures suggestive of sensory organs but seeming to have no very definite epithelial relationship. This body, though figured by Rossi (1902) and Effenberger (1909) has apparently received no special name, but might be referred to as the dorsal pharyngeal eminence. It is essentially similar in all the Diplopods which I have investigated though proportionally larger and more conspicuous in the three Polydesmoids than in Parajulus. (See Figures 5, 6, 7 and 10).

Arising laterally from the ventral wall of the pharynx near the point where it is continuous with the distal margin of the hypostoma (Silvestri, 1903) and projecting dorso-cephalad, are a pair of rounded plates, the internal maxillary laminae (Silvestri, 1903), which resemble the somewhat ventrally projecting margins of the dorsal anterior laminae and with them serve to close the mouth opening when the mouth parts are adducted. Like the anterior laminae, they too have a marginal row of spines, but here the spines continue as parallel supporting rods to the base of the plates thus giving them a dainty comb- like appearance. In Fontaria, the internal surface of the maxillary laminae is markedly setaceous, while in Parajulus, Scytonotus and Orthomorpha there are only a few distal emergencies.(See Figure 71).

Situated medially and internally on the distal margin of

the hypostoma, are a pair of rounded bodies bearing pits and known as the lobi linguales (Latzel,1880). Extending posteriorly from these is a midventral strip, flanked laterally by a row of spines and bearing numerous smaller spines and fungiform emergencies. Anteriorly this strip is distinctly elevated in the form of a blunt ridge and, near the posterior end of the pharynx, there is a similar elevation which abruptly divides into two ridges that circumvent a pronounced pocket or depression already referred to. Posterior to the latter and immediately ventrad of the oesophageal opening, the two ridges come together again to form another setaceous eminence which partly overlaps the pocket. Within the pocket itself is a structure which Silvestri has named the prepharynx and which shows such distinctive differences in the four genera that it deserves special mention. (See Figs. 6, 7, 8 and 9).

(b) Prepharynx

The prepharynx has been described by Silvestri (1903) in all the important groups of Diplopods but seemingly no attempt has been made to study it histologically in relationship to the underlying epithelium or to ascribe any function to it. It apparently reaches its greatest development as regards both size and complexity in the Juloid Diplopods, and particularly in Pachjiulus Communis (Savi), where the entire structure has over half the width of the hypostoma and comprises two blade-like lateral pieces medially united to a thick, rounded central body or corpus. It thus roughly describes a figure H. with the corpus projecting somewhat caudad from the point where it unites with the lateral pieces, and with a pair of slender

anterior cornua extending distally from the anterior margin of the corpus. In an unidentified species of Julus from New York State, I found the prepharynx essentially as described by Silvestri for Pachyiulus and, upon dissection, noted that the anterior cornua functioned as apodemes for the attachment of muscle fibers arising from the hypostoma.

In Parajulus the prepharynx is distinctly smaller than in Pachyiulus, having only one third the width of the hypostoma, but is otherwise quite similar. The anterior cornua, however, are inconspicuous though serving for the attachment of muscles as in the above mentioned Julus. When examined fresh the corpus is of a bright yellow color, but this very quickly disappears if the head is skeletonized in potassium hydroxide. When examined sectionally, the lateral pieces are seen to be masses of secondary chitin lying snuggly against the primary chitin of the intima, which bears pores that do not appear to traverse the secondary and which is elevated into a spinous projection at each side of the corpus. The latter is apparently a special modification of the primary chitin and has a striated aspect very suggestive of minute pore canals. (See Figs. 6, 8A , 8 C, and 11A.)

The three Polydesmoid genera are alike in having lateral prepharyngeal pieces of the same color and much the same texture as the corpus of Parajulus. But the striations are not so canalicular and the yellow is much more resistant to potassium hydroxide. In Scytonotus and Orthomorpha they are distinctly trabecular in shape, while in Fontaria each has a blunt, medially projecting process arising from its posterior part. They appear

to be formed exclusively of primary chitin and are so unlike the lateral pieces of Parajulus that they immediately suggest a homology with the corpus of the latter. The corpus is represented, in position at least, by structures which are quite distinctive in each genus and which are brought out in Figs. 7, 9, 11A, C and D, with sufficient clearness to make further reference to them unnecessary. Suffice it to say that the round, thickened posterior region of the Fontaria corpus is the only part resembling the corpus in Parajulus.

(c) Tentorium.

Silvestri (1903) describes as the tentorium of Pachyiulus, a paired, chitinous structure situated in the head caudo-lateral of the pharynx and comprising two main parts; a pars ascendens tentorii with its long axis dorso-lateral and a pars transversalis tentorii, which bends directly lateral from the summit of the first part and attaches to the posterior incisura of the clypeus just behind the base of the antenna. From the obtuse angle formed by the junction of these two parts arises a small process, processus superior internus tentorii which extends dorsomedially toward the roof of the pharynx. A similar process, processus inferior internus tentorii, projects mesiad from the ventral portion of the pars ascendens and articulates broadly with the posterior end of the prapharyngeal lateral piece, while from the same level of the pars ascendus a large, clavate processus posterior tentorii projects caudad toward the dorso-lateral margin of the pseudocciput but ends freely at an appreciable distance anterior to this. Silvestri concludes his discussion

with the statement that the tentorium is essentially the same in all Chilognaths, but that it is shorter and thicker and the posterior process markedly shorter in the Polydesmoids than in the other groups.

Berlese (1910, Page 454) refers to Silvestri as claiming that the median, chitinized central tendon, which serves as a common point of attachment for the adductor muscles of the mandibular cardines, stipites and premandibles, enters largely into the composition of the tentorium. On this basis he suggests that the central tendon may be homologous with the corpus tentorii of insects. I shall touch upon the question of homology later on.

The tentorium of Parajulus is so similar to that of Pachyiulus that it will not be necessary for me to describe it in detail. Consequently I shall confine myself to a few observations not covered by Silvestri. In the first place, I find that the processus superior internus tentorii is attached at its extremity to the pharyngeal intima dorso-laterally, a little anterior to the posterior end of the pharynx. I also find that the premandibular apodeme passes directly above the superior process in extending caudad and is attached to the same by a few minute chitinous tendons. The pharyngeal epithelium is continuous over all parts of the tentorium as a very flat, sometimes hardly perceptible layer and, at the point where the pars transversalis unites with the exoskeleton, it is continuous with the hypodermis. Except for this continuity with the latter, a similar epithelial relationship appears to hold true for the other three genera and in consideration of the epithelial origin

of chitin, it is difficult to conceive of any other possibility.

From what has been said previously, it will be noted that in Parajulus the posterior process is the only part of the tentorium which does not end in an attachment to some other chitinous structure but, extending obliquely caudo-medial from this process near its base, is a small projection which unites on each side with the central tendon and thus corroborates Berlese's statement in regard to the latter entering into the composition of the tentorium. Solid midventrally, it extends dorso-laterally for a considerable distance as a light, irregularly partitioned, chitinous framework which seems to serve merely as a device for allowing greater space for the tendinous attachment of the adductor muscles of the mandibles and appears to end freely near the dorso-lateral wall of the cardines. (See Figs. 5 and 11A).

In agreement with Silvestri's statement regarding Polydesmoids in general, the tentoria of Scytonotus, Orthomorpha and Fontaria are more massive and less ramose than in Parajulus, but very much alike in the three genera. The part which I have recognized as the inferior process attaches ventro-lateral instead of caudad to the lateral prepharyngeal pieces and, though firmly united with the remainder of the tentorium, it is clearly marked off from it by a distinct suture. Dorsally it is broadly united with the pharyngeal intima which, in both cross and longitudinal sections, is seen to present a slightly concave, porous surface at this point and is therefore strongly suggestive of the intima above the lateral prepharyngeal pieces in Parajulus. (See Fig. 9- P. I. T.).

This would tend to strengthen the suggestion made earlier, that the lateral prepharyngeal pieces of the Polydesmoids are homologous with the corpus of Parajulus and that the inferior tentorial processes of the former represent the lateral prepharyngeal pieces of the latter. From the inferior process, the remainder of the tentorium extends dorso-laterally but presents no angle dividing it into ascending and transverse parts. Although its dorso-lateral extremity is free, I have recognized it as equivalent to the pars transversalis of Parajulus, and a short process arising from a point just lateral of the inferior process and uniting dorso-laterally with the pharyngeal intima, I have considered with better reason as the superior process. At a point along the main axis of the tentorium about midway between its two extremities, another short process projects caudo-mediad and unites laterally with the central tendon as in Parajulus. This union was brought out very clearly in serial transverse sections through the head of Orthomorpha. For Scytonotus and Fontaria my sectioned material was insufficient to demonstrate it, though all indications pointed that way. It would appear, then, that this process is all that represents the posterior process of the tentorium in these three Polydesmoids, but it must be further observed that the free pars transversalis occupies a position intermediate between the attached pars transversalis and free posterior process of Parajulus and, moreover, that it serves for the attachment of many of the muscle fibers from the mandibular stipes; a function which seems to be subserved only by the posterior process in Parajulus.

Regardless as to whether the Juloid or Polydesmoid type of tentorium is the most primitive, at least two possibilities are here suggested.

1. That what I have been considering as the pars transversalis of these Polydesmoids is really the posterior process, the former being absent.

2. That the pars transversalis is present but serves as the Juloid posterior process while the true posterior process is merely a connecting link between the central tendon and tentorium proper. Finally, it is well to note in this connection that in Parajulus the posterior process serves also as an attachment for muscles extending laterad from the anterior part of the oesophagus while in Fontaria and Orthomorpha, as based on observations of dissected and sectioned material, the premandibular apodeme bears a similar relationship to muscles analogous to the others in function and position. (See Fig.11. B, C and D.).

In attempting to homologize the Diplopod tentorium with that of insects, one's path is beset with difficulties. At first consideration, the partes transversales of Parajulus might be readily identified with the dorsal arms of the insect tentorium since both attach near the base of the antennae, and the posterior processes with the posterior arms of the latter inasmuch as they follow somewhat the same course toward the posterior part of the head. Also the superior processes might be correlated with the anterior arms in insects because of their relationship to the premandible in the first case and

mandible in the second, and the ventral, medially directed inferior processes or, possibly the central tendon, with the insect corpus tentorii. But in the light of the observations of Comstock and Kochi (1902) on the tentoria of Orthoptera, Neuroptera, Hymenoptera and other orders, it would appear that the posterior arms originate as outgrowths from maxillary pleurites which unite with the anterior arms in forming the corpus, while the dorsal arms, reduced or absent in many insects, develop as outgrowths from the corpus to the bases of the antennae according to Riley (1904). In Diplopods, however, if one is to judge from the relationship of the pharyngeal epithelium which I have referred to as completely investing the tentorium, the conditions would seem to be just the reverse; for in this light the posterior processes would appear to have originated as anterior outgrowths reaching backward rather than posterior outgrowths reaching forward. Moreover the partes transversales are apparently the only elements which could have developed as ingrowths from the outer parts of the head.

(d) Epithelium.

In all four genera, the pharynx is lined by a conspicuous epithelium which varies in thickness very much in accordance with the thickness of the underlying intima. It is therefore quite thick on the dorso-medial and ventro-medial surfaces where it averages between 10 and 15 microns in Parajulus and Fontaria and between 9 and 12 in Scytonotus and Orthomorpha, but is thickest of all within the premandibles where it is gathered into a number

of irregular folds which always stain darker than the other parts of the epithelium and, in a fresh condition, appear uniformly light brown owing to the presence of a fine, brown granulation within the cytoplasm. Elsewhere the epithelium is cuboidad or flat, especially in the caudo-lateral region of the pharynx where it invests the tentorium and always appears more or less receded from the intima. It is probable that this latter condition is due entirely to poor fixation.

Rossi (1902), Krug (1907), Effenberger (1908), Wernitzsch (1910) and Reinecke (1910), figure the pharyngeal epithelium in mid-sagittal views of the head but say very little about it, and, except in its relations to the masticatory plates of the premandibles and the prepharynx, it presents no very distinctive features in my specimens. The cells of the dorsal and ventral walls of the pharynx are columnar with a width of about one fourth or one fifth of the length. The nuclei are usually well rounded, clear and situated in the basal third of the cells, while the cytoplasm is either homogeneous or presents a fine spongioplasmic reticulum which sometimes shows a few distinct vacuoles. A thin, structureless basement membrane can be readily seen, especially when Mallory's stain is used. (See Figs. 6, 7, 8A, and 9.).

Directly beneath the masticatory plates of the premandibles, the cells are distinctly fusiform and taper distally into thread-like processes that occupy the central parts of the pits mentioned in a former paragraph. Proximally they appear to be continuous with nerve fibers and in one instance

traced their connections with a well defined nerve. Their protoplasm appears quite similar to that of the adjacent epithelial cells, but their nuclei are very elongated and take a dark stain. Because of their relationship to the pits which bear a close resemblance to Schenk's (1903) sensillum ampullaceum in the honey bee, I have little doubt that these are sensory cells. A somewhat similar relationship seems to obtain in Parajulus between the pore canals of the prepharyngeal corpus and the underlying epithelium, but here the cells, aside from being narrower and more densely massed, are very much like the typical columnar cells and their affinity with sensory cells is much more doubtful than in the former case. In the other genera they are even less suggestive of sensilla than in Parajulus. (See Figs. 8.B and C.).

(e) Suspensory Muscles.

The suspensory muscles of the pharynx seem to show very much the same positions and relations in every instance in which they have been figured or described, as well as in the four species under consideration. For this reason, and especially because Silvestri's(1903) description of the muscular system of Pachyiulus includes a very thorough treatment of the pharyngeal muscles, I shall give them only brief mention here.

The upper ones, superior dilators, insert on the dorsal wall of the pharynx in four well defined and evenly spaced groups which extend all the way across. Of these, the first attaches a very short distance posterior to the mouth opening

and the last at a level immediately anterior to the brain. In the two intermediate groups, the fibers pass through the anterior salivary glands which lie dorsad of the pharynx and cephalad of the brain and, as one might reasonably expect, there is sufficient space between the individual fibers and the glandular tissue to allow for the free functioning of the former. The fibers of the first three groups are relatively few and far apart as compared with the last which is, in consequence, the most conspicuous and important of the four.

Except for a few anterior fibers, the inferior dilators comprise a single bundle which inserts caudo-ventrally on the pharynx and originates on the hypostma at a level about one third of the distance from its base to its distal extremity. (See Figs. 6, 7, 8.A, and 9.).

(f) Summary.

1. The prepharynx of Parajulus is very similar to that of Pachyiulus, as described by Silvestri, but markedly different from that of Scytonotus, Orthomorpha and Fontaria, and the corpus in the former may be homologous with the lateral pieces in the other genera.

2. The tentorium of Parajulus is distinctly different from that of the Polydesmoid genera, but it is possible to indentify in the latter all the parts that are recognized in the former.

3. The central tendon is connected with the tentorium proper in Parajulus and Orthomorpha, and probably in the Scytonotus and Fontaria as well.

4. The homology of the parts and processes of the Diplopod

with the arms of the Hexapod tentorium is very doubtful.

5. The cells underlying the masticatory plates of the premandibles are probably sensory and a sensory function is suggested by the structure of the prepharyngeal corpus in Parajulus.

6. The suspensory muscle fibers are similar in all four genera and the superior dilators are disposed in four clearly defined groups, while the inferior dilators compose but a single group.

B. Oesophagus.

In its general features, the oesophagus corresponds very closely in my four genera to the observations made upon it elsewhere. Although varying slightly under different states of muscular expansion and contraction; its macroscopic appearance is quite constant in Scytonotus, Orthomorpha and Fontaria, where it shows a perceptible decrease in diameter in the posterior region of the head and thence a gradual increase back to the point where it unites with the midgut or cardiac valve. But in Parajulus, while conforming in the main with the others, its posterior third is often expanded to about twice its usual, average diameter and thus forms a rather vaguely defined, temporary crop which tapers gradually at each end.

When in a fresh condition, the oesophagus appears semi-transparent or somewhat gelatinous in the Polydesmoid genera, but of a dark, violet color in Parajulus, due to the presence of pigment granules in the epithelium and of varying intensity in dif-

ferent individuals. In the cephalic region of the oesophagus, the color is usually very faint or entirely absent. Apparently this pigmented condition of the epithelium is not a generic but a specific character occurring here and there throughout the Juloidea, since I have found no evidence of it in other species of Parajulus which I have examined and since Plateau (1878) notes its presence in Julus sabulosus and terrestris and its absence in Julus Londinensis. (See Figs. 1-2-3-4).

(a) Intima.

The oesophagus is lined by a smooth non-porous intima which shows no marked changes in thickness throughout its course but which becomes gradually thinner in the region of the cardiac valve and ends almost imperceptibly where the mid intestinal and oesophageal epithelia unite. Along the greater part of its course it is disposed in six rugae, and thus far agrees with the figures and brief descriptions of Krug (1907), Effenberger (1909), Reinecke (1910) and Wernitzsch (1910). Wernitzsch notes that the rugae of Craspedosoma are regular and that they are absent anteriorly but become more and more prominent posteriorly. This accords quite well with what I have observed in Parajulus and Orthomorpha where I have been able to follow the entire course of the oesophagus in serial cross sections and noted the following changes in shape. In both forms, the oesophageal lumen at its anterior end is trapezoidal in shape with its greatest width anterior but presents three symmetrical pairs of sharp folds; one dorsal, one dorso-lateral and a third ventro-lateral. (See Fig. 12.A.). At this point the oesophagus is distinctly

wider than thick but, immediately posterior to the brain, the lumen is of even diameter while the folds have become curved as shown in Fig. 12.B. Still farther caudad and at a point a little forward of the pseudocciput, the folds are still symmetrical but, at the intervals between the dorso-lateral and ventral ones, the intima has become sharply bent in, thus assuming the appearance of typical rugae. (See Fig. 12.C.). Just posterior to this the intervals between the dorsal and dorso-lateral folds bend in in like manner and form three more rugae similar to the first. Caudad of this point and continuous throughout the remainder of the oesophagus, the rugae become markedly irregular both as regards size and shape and especially so in Parajulus. At the apices of the rugae, the intima is thicker than elsewhere and quite sharply angular and, in some of my specimens stained with Mallory, is differentiated into a homogeneous ental and granular proximal zone, suggestive of what Van Gehuchten (1890) has observed in the larva of Ptychoptera contaminata. (See Fig. 13.). Just anterior to the cardiac valve the rugae become blunter, more rounded and decidedly more symmetrical while in Parajulus, when this region is fully expanded, they are entirely obliterated but reassert themselves farther caudad and within the cardiac valve itself. (See Figs. 14, 15, 16, 17, and 18.).

(b) Epithelium.

The epithelium in all four genera is essentially similar to that of the other Diplopods in which it has been studied, with the exception of Polyxenus lagurus in which Reinecke (1910)

pictures the cells as proportionally very large and only about nine or ten to the cross section. Directly continuous with the pharyngeal epithelium and showing no abrupt transition in its connection with the same, it begins anteriorly as cuboidal and thence becomes gradually thicker caudad, showing an average increase from the pharynx to a point just anterior to the cardiac valve, of from 8 to 35 microns in Parajulus, 7 to 12 in Scytonotus, 7 to 18 in Orhomorpha and 25 to 40 in Fontaria. In the Polydesmoids, as also in the cephalic portion of the Parajulus oesophagus, the cytoplasm appears to be very similar to that of the thicker areas of the pharyngeal epithelium while the nuclei, round in the cuboidal cells but slightly elongated in the columnar, are proportionally small and contain karyosomes which vary somewhat in the different stains but usually appear diffuse and irregular. The epithelium in the trunk portion of the oesophagus of Parajulus varies very much in accordance with the number of pigment granules within the cells. When these are few, they almost always appear quite uniformly distributed throughout the cell but when abundant, are concentrated in more or less irregular masses in the distal or proximal parts, while in the vicinity of the nucleus the cytoplasm is often clear or vacuolated. (See Fig. 15). Within the cardiac valve, the pigment granules are either very diffuse or entirely lacking. As I have already intimated, the amount of pigmentation varies in different individuals but, with the possible exception of the early larval stages which are beyond the extent of my observations, there is apparently no correlation between age and number of granules,

since I have found a denser pigmentation in 14 mm. larvae than in some of my sexually mature specimens. In all the genera the basement membrane is simple and structureless as in the pharynx. (See Figs. 12 to 18).

(c) Suspensory Muscles.

The suspensory muscles which attach the cephalic portion of the oesophagus to the head need not be described in much detail here, inasmuch as they are apparently similar in all Diplopods and have been thoroughly described by Silvestri (1903) in Pachyiulus. They may be conveniently divided into superior, inferior and lateral dilators. Of these, the superior form a very distinct bundle which is practically continuous with the last pharyngeal group of dilators at its insertion, though separated at its origin on the vertex by the interposition of the brain. Anteriorly the bundle is quite dense and distinctly fan-shaped, but continuous caudad as far as the pseudocciput in the form of relatively sparse fibers dorso-laterally attached to the oesophagus. The inferior dilators originate, for the most part, on the dorsal surface of the central tendon, but posterior to these are a few sparse groups of fibers that insert ventro-laterally on the oesophagus and thence pass caudad to a ventro-lateral origin in the vicinity of the basilar plate of the hypostoma, which forms the ventral margin of the pseudocciput. Inserting laterally on the oesophagus in two pairs of wing-like groups, are the lateral dilators. Of these the first pair, as I have already noted in a previous section, originates in Para-

julus on the posterior processes of the tentorium and analogous muscles in Orthomorpha and Fontaria, on the premandibular apodemes. In the latter case, because of the more dorso-lateral position of the apodemes, the fibers extend cephalo-laterad in attaching to them; whereas in Parajulus with its posterior processes almost parallel to the oesophagus their analogues extend directly laterad. The posterior pair of lateral dilators originate on the lateral margins of the pseudocciput, and at least two pairs of fibers which pass caudo-mediad to the oesophagus continue for some distance posteriorly as inner longitudinal fibers of the muscularis. Insofar as I have been able to determine, this is the only place in Parajulus and Orthomorpha where the suspensory muscles directly contribute to the formation of the muscularis, though they often insert so broadly along the sides of the oesophagus that they might be easily recognized as continuous with circular or longitudinal fibers. (See Fig. 12. A, B, C and D.).

(d) Muscularis.

Krug (1907), Effenberger (1909), Wernitzsch (1910) and Reinecke (1910) all refer to the oesophageal muscularis as comprising a weakly developed, inner longitudinal and a strongly developed, outer circular layer, and this is precisely the condition which obtains in my specimens, though my observations on Scytonotus and Fontaria have been more limited than on Parajulus and Orthomorpha. As regards the inner longitudinal fibers, I am uncertain as to their full or maximum number, but have never been able to identify more than twelve in any one cross section.

Throughout the middle third of the oesophagus they tend toward an arrangement in pairs at the bases of the rugae, but often there is only one at the base of each and sometimes three may occur under one ruga and none under some of the others. In the Polydesmoid genera they extend the entire length of the oesophagus but show no consistent increase in numbers from beginning to end nor any clear indication of branching, and, since I have been able to find no correlation between them and the outer longitudinal fibers of the midgut, I can only conclude that they end at the cardiac valve. In Parajulus they seem to begin at the anterior end of the oesophagus as five dorsal and two or three ventral fibers, and in both Parajulus and Orthomorpha, as I have already mentioned, two pairs of lateral ones are added as continuations of suspensory muscles originating laterally on the pseudocciput. Apparently their extent is limited to the anterior two thirds of the oesophagus in Parajulus since I have found no trace of them in the posterior region which forms the temporary crop. These fibers are always relatively large, with an average diameter of from 6 to 9 microns in Parajulus, Scytonotus and Orthomorpha and from about 10 to 15 in Fontaria. In the few instances where I have seen them well in longitudinal section they appeared striated. (See Figs. 12, 13 and 15.).

The outer circular layer extends the entire length of the oesophagus as a very uniform ring of contiguous fibers which are of about the same caliber as the inner longitudinals and are always striated, as opposed to Reinecke's (1910) contention that the oesophageal muscles of Polyxenus are smooth. Except over the cardiac valve where a more or less clearly defined

sphincter may be recognized, they are always disposed in a single layer and at infrequent intervals show branchings which always inter connect the fibers at oblique angles. (See Fig. 19.).

At about the mid region of the oesophagus in Orthormorpha but quite near the posterior end in Parajulus, may be seen a few, irregularly distributed outer longitudinal fibers which, by branching repeatedly in their course caudad of these levels, form a well defined outer longitudinal layer. Its fibers in Scytonotus and Fontaria probably originate at the same level as in Orthomorpha, but, since my cross sections of the former include only the posterior parts of the oesophagus, I am unable to verify this point. In all four genera this layer bridges over the cardiac valve and thence continues posteriorly as the outer longitudinal layer of the midgut. The fibers always have a smaller diameter than the circular or inner longitudinals and this gradually decreases as they proceed caudad until the midgut is reached.

It will be seen from the foregoing that in the Polydesmoid genera the inner and outer longitudinal layers overlap each other, but nowhere have I seen anything to indicate an interconnection between the two, such as Balbiani (1890) has described for the Chilopod, Cryptops. On the other hand, in Parajulus at the region where the crop-like expansion may take place, there is apparently a well defined interval between the points where the inner longitudinals end and the outer begin. This not only favors the belief that the two layers are separate but is also in accord with the condition which Anton Schneider (1887) presents as typical for Insecta. Moreover, with both sets of fibers under contraction, it is obvious that the interval between them would

be the logical place for an expansion to occur, and, in like manner, the overlapping of the two layers and especially the continuation of the inner longitudinals to the cardiac valve, might explain the apparent absence of an expanded area in the Polydesmoid oesophagus. (See Fig. 16.).

(e) Cardiac Valve.

In the four genera under consideration, as well as in the other Diplopods which have been noted in this regard, the cardiac valve appears essentially as a simple pouching of the oesophagus into the anterior extremity of the midgut and is thus very much like homologous regions as they exist unmodified in Insecta and other groups of Arthropoda. When viewed in sagittal section, the oesophageal wall is thus seen to be reflected on itself and beyond this reflection the epithelium continues cephalad for some distance before uniting with the midgut epithelium, while this unfolding includes the oesophageal wall in its entire circumference, the apices of the six rugae project farther caudad than the intervening areas and it is chiefly to the former that one refers collectively in designating the cardiac valve.

As figured by Krug (1907), Effenberger (1909), Wernitzsch (1910) and Reinecke (1910), the oesophageal epithelium shows no very noticeable increase in thickness at the apices of the valves and in this respect resembles Scytonotus and Orthomorpha where it never exceeds 20 microns, but in Polydesmus between the valves proper and the commencement of the midintestinal epithelium, Effenberger figures a region of columnar cells which is distinctly

higher than the remainder of the oesophageal epithelium and in which the nuclei are described as 'involuted'. In none of my specimens have I noticed anything comparable to this, though in Parajulus and Fontaria, the epithelium is markedly higher at the apices of the valves than elsewhere in the oesophagus, having a thickness of from 40 to 50 microns in both or even 60 in Parajulus. With the exception of Polydesmus, the oesophageal epithelium narrows down perceptibly toward the point where it makes contact with the midintestinal epithelium. (See Figs. 20, 21, 22 and 23.).

The valves of the Parajulus, which I have studied in a greater number of individuals than in the other genera, vary from short and well rounded to long and sharply angular infoldings, and the cause of this variation may be readily identified with the functioning of the outer longitudinal muscle fibers. Moreover, it will be seen in Fig. 20, that the circular layer not only shows no thickenings worthy of the term, sphincter, but does not even extend down into the folds of the valves. This, together with the foregoing observation, would justify the conclusion that in Parajulus the cardiac valve is a device for enabling the oesophagus to become shortened by the contraction of the longitudinal muscles without bringing undue pressure to bear on its epithelium, as well as a valve in the true sense of the word. In Scytonotus and Orthomorpha, as also in Craspedosoma, Julus, Polydesmus and Polyxenus, there are no clearer indications of a sphincter than in Parajulus, though, as a result which might readily follow from the contraction of the longitudinal fibers,

a few of my Orthomorpha slides show the circular layer extending a short distance into the cardiac folds. Fontaria, however, presents a well defined sphincter with a thickness comprising three or four tiers of fibers and situated at the base of the valves. (See Figs. 20, 21, 22 and 23.).

Krug, Effenberger and Reinecke refer to the presence of connective tissue within the folds of the valves, and, wherever the inner and outer walls of the folds were sufficiently separated from each other, I also have observed it, but in Parajulus and Fontaria, in addition to the ordinary diffuse connective tissue, there is present well at the base of the valves an unbroken ring of rather densely massed round cells. This ring is closely invested by the basement membrane which divides in surrounding it, while its cells have a relatively large, round or oval nucleus centrally situated and an uneven, slightly granular cytoplasm. Interspersed among the latter, I have found in Parajulus triangular packets of much smaller cells which, because of their poorly defined cell boundaries, are very suggestive of germinal cells. But, inasmuch as this ring of cells is separated from the epithelium by the basement membrane, it is very doubtful if it has anything in common with the stomodeal imaginal rings of insects which are the regenerative centers of the oesophageal epithelium and which are described by Verson (1898), Kowalevsky (1887) and others in Lepidoptera and Diptera larvae as forming an integral part of the oesophageal epithelium at the point where it unites with the midintestinal and hence lying entad of the basement membrane. Moreover, some of my Parajulus

sections show bud-like clusters of small cells situated at the junction of the two epithelia and therefore analagous if not homologous with stomodeal imaginal rings. (See Fig. 20.). In some of my iron haematoxylin preparations of Parajulus, the cells of the outer ring are quite suggestive of muscle fibers, but their reaction to Mallory's stain is altogether different. Thus, besides hinting at a possible glandular function, I can merely affirm that this structure represents something more than ordinary connective tissue. (See Figs. 20 and 23.).

(f) Summary.

1. The rugae of the oesophagus are six in number and more or less irregular throughout the greater part of their extent in all four genera.

2. The oesophageal epithelium of Scytonotus, Orthomorpha and Fontaria is colorless in a fresh state, but contains pigment granules which give it a deep violet color in Parajulus venustus. These granules vary in number in different individuals but apparently without regard to sex or age.

3. The anterior group of lateral dilator muscles of the oesophagus originate on the posterior processes of the tentorium in Parajulus, but analogous muscles originate on the premandibular apodemes in Orthomorpha and Fontaria.

4. The outer longitudinal muscle fibers of the midgut continue cephalad along the walls of the oesophagus for some distance in all four genera.

5. The inner longitudinal fibers extend the entire length of the oesophagus in Scytonotus, Orthomorpha and Fontaria and thus overlap the outer longitudinals, while in Parajulus there is an interval between the ending of the inner longitudinals and the beginning of the outer, which by the contraction of both sets of fibers may become expanded and take the form of a crop.

6. The outer longitudinals increase in number posteriorly by branching and the circular fibers branch to a limited extent, but the outer longitudinal, circular and inner longitudinal layers show no interconnection with each other at any point.

7. In Fontaria there is a well defined sphincter muscle at the base of the cardiac valve, but this is not apparent in the other genera where, especially in Parajulus, the valvular function of the cardiac valve is probably supplemented by that of providing room for the excess intima and epithelium when the oesophagus is shortened by the contraction of the longitudinal muscle fibers.

8. In Parajulus and Fontaria there is a well defined ring of small, round cells which invests the oesophagus at the base of the cardiac valve and which may have some regenerative or glandular significance.

3. Midgut.

As previously intimated, the midgut in whatever Diplopod it has been observed, always takes the form of a simple tube without diverticula or appendages of any sort, but in the four genera under consideration as well as in the three species of

Julus studied by Plateau, the caliber of the tube varies noticeably throughout its length depending largely on the amount and distribution of the food matter within its lumen. This variation which is sometimes quite slight in well filled midguts of Parajulus, Scytonotus and Orthomorpha, appeared constant and always very conspicuous in the relatively few Fontaria midguts that I have been able to examine. Here in a region a short distance posterior to the cardiac valve and in another just anterior to its caudal extremity or pyloric valve, they were expanded to a diameter of 4 mm. but narrowed down in the intervening areas to one of 1.5 or 2 mm. As I shall point out later on, this great variation in diameter is probably closely associated with a modification of the longitudinal muscles not observed elsewhere in Diplopods. In the contracted intervening areas, and especially noticeable just cephalad of the pyloric valve, the midintestinal wall of Fontaria is often elevated into a series of more or less prominent circular folds, which, when viewed in a sagittal section, are seen to involve the epithelium and basement membrane to a greater extent than the outer layers. Contrasting markedly with the condition noted above the midgut of Glomeris, according to Plateau (1878) is either uniformly contracted or uniformly expanded. (See Figs. 1, 2, 3 and 4.).

A. Peritrophic Membrane.

The peritrophic membrane, known for a long time in insects, was apparently first identified in Diplopods by Visart (1895) who in Julus, Tropisoma, Polydesmus, Lysiopetalum and Glomeris

adopted Schneider's (1887) view in interpreting it as a direct posterior continuation of the oesophageal intima and hence secreted by the oesophageal epithelium. Krug (1907), Effenberger (1909), Wernitzsch (1910) and Reinecke (1910) make no mention of it at all, though Krug refers to the anterior part of the midgut of Julus as having a cuticula which is lacking in the hinder part. Léger and Duboscq (1904) say nothing about it but figure it in Craspedosma Rawlinsii simile, Verh.

In dissections of all of my genera, I have constantly encountered it as a membranous tube extending the entire length of the midgut and often on into the hindgut for a considerable distance. At places it often appeared quite definitely united with the midintestinal epithelium, but was separated from it elsewhere by an appreciable cavity. It always enveloped the food matter rather closely, and sometimes in the midgut but invariably in the anterior part of the hindgut, it was greatly constricted and wrinkled at intervals where its lumen was devoid of solid particles. The faeces of Parajulus and Fontaria were always invested by segments of the peritrophic membrane which for some time prevented the disintegration of the former when placed in alcohol or water. Under similar tests, the faeces of Scytonotus and Orthomorpha immediately disintegrated and upon examining them I found that, while the peritrophic membrane was present, it was greatly torn and presented many small and unevenly distributed punctures. This led me to infer that the intima of the hind intestine in these genera must possess spines or teeth, and subsequent investigations have proved this to be correct, as I

shall point out later on. (See Fig. 55.).

That chitin enters largely into its composition, I was able to demonstrate by finding that the membrane was resistant to strong solutions of potassium hydroxide after immersion for indefinite periods of time. I also found that, when the oesophagi were included with the midguts subjected to the solutions, the peritrophic membrane always remained attached to the intima of the former and since the basement membrane is non-resistant to the potassium hydroxide, it is very unlikely that it took part in this attachment. Thus I am in agreement with Visart, to the extent of admitting that it is continuous with the intima of the oesophagus. But it must be further noted that all of the peritrophic membranes which were treated with the potassium hydroxide showed a much greater average thickness posteriorly than anteriorly and that, wherever thickenings occurred, they always consisted of additional membranes, peripheral to the older ones and interconnected with them. This at once casts doubt on the supposition that the membrane is secreted by the epithelium of the posterior end of the oesophagus, for were this the case, one would expect to find a single membrane of practically uniform thickness, and the addition of new chitinous parts at points posterior to the secreting cells would be a logical impossibility. Even granting that the oesophageal cells secrete more actively at certain times than at others, it is obvious that a limited chitinogenous area would scarcely be able to add new increments along the sides of a constantly receding membrane.

I have already noted that at certain irregular intervals along its course, the peritrophic membrane appeared closely adherent to the mid-intestinal epithelium. Sections through such areas in all four genera show a very definite continuity between the membrane and the epithelium and thereby indicate that here and not in the epithelium of the oesophagus is the source of the former to be found. But since this first will be touched upon again in connection with the epithelium, I shall close this topic for the present by declaring that all my observations lead me to the following conclusions; that the peritrophic membrane is secreted by the midintestinal epithelium, that while all the mature cells are capable of this function only limited areas of the epithelium are performing it at a given time, and that the membrane increases its length by being alternately torn apart and renewed in regions where excessive strain is momentarily brought to bear upon it. This is essentially similar to the theory enunciated by Plateau (1874) and supported by Balbiani (1890), Verson (1898) and others, regarding the origin of the peritrophic membrane in insects. Finally, as regards the connection between the latter and the oesophageal intima, it might well be argued that, since the underlying epithelia interconnect, it is reasonable to suppose that their secreted products when of a similar nature would tend to interconnect also.

B. Epithelium.

In general, the midintestinal epithelium of Diplopods in every instance in which a detailed study has been made of it,

is in conformity with the typical plan of structure encountered in Insecta and other groups of Arthropoda. This is characterized by the presence of three kinds of cells; small cells with proportionally large nuclei and inconspicuous cytoplasm which are largely confined to the basal part of the epithelium, large cells which are usually narrow at their point of attachment to the basement membrane but present a more or less extensive flat or convex ental surface lined by a cuticula, and, lastly, cells which are even more constricted basally than the preceding but are dilated entally in the form of either single, large spheres often containing the nuclei or a number of small spheres party or wholly constricted off from the remainder of the cells. Of these three kinds, the small basal cells vary greatly in their manner of occurrence within Arthropoda, but in all, three main types of distribution may be recognized. In the first place, they may be diffusely disposed along the basement membrane, either at wide intervals from each other or so close together that they form a fairly continuous layer throughout the midgut. This is the condition met with in many larval insects, especially Lepidoptera and Diptera (See Verson, 1898 and Van Gehuchten, 1890), in Decapod Crustaceans (See Frenzel, 1885, A.) and in Diplopoda (See Visart, 1898 and Léger and Duboscq, 1904). Secondly, they may occur in well defined clumps or nidi which usually show quite a symmetrical arrangement and which may be found in most adult insects and many hemimetabolous larvae (See Miall and Denny '86, Faussek '87, Oudemans '87, Needham '97 and Imms 1919.) as well as in Chilopoda and Arachnida to a limited extent. (See Bal-

biani, '90, Sograff '79 and Berlese, 1901). Thirdly, they may be present in crypts or sack-like evaginations from the midintestinal wall, as in many adult Coleoptera especially the Hydrophildae and Dytiscidae. (See Bizzozero, 1893 and Rengel, 1897). The two kinds of large cells present no descriptive differences which might be used as a basis for distinguishing the classes or orders of Arthropoda, although in Chilopoda they seem to be more attenuated and fusiform than elsewhere. (See Balbiani, 1890).

The functions attributable to the midintestinal epithelium have been much in dispute for the last four or five decades, but, though there are many specific problems still unsolved, a general agreement has been reached regarding the interrelationship of the three kinds of cells. A brief mention of some of the most important interpretations that have been placed upon the latter will help toward a clearer understanding of what follows. Frenzel (1885 B.) and Faussek (1887) looked upon the nidi or clumps of small cells as special secretory glands and figured what they conceived to be their ducts opening into the lumen through minuted pores. They also held that the cells of the nidi reproduce by mitosis and the large, enveloping gland cells by amitosis, and used this observation as a basis for denying any genetic relationship between the two. Schiemenz (1883) regarded the small cells as glandular, but recognized the large ones as absorptive rather than secretory. Miall and Denny (1886), in comparing the small cells of the cockroach with seemingly analogous cells in the intestinal epithelium of mammals, reached the conclusion that the former are regenerative and, in so doing, established the view which has been generally accepted from that time on to the present

and which might be stated as follows:

1. The three kinds of cells are genetically interrelated and thus represent three successive stages in the life cycle of but one kind.

2. The small cells proliferate by mitosis and develop pari passu into the large cells with a cuticular border by a process of elongation until their free ends reach the lumen. Having then acquired a cuticular border, they become functionally mature and have been oten referred to with doubtful propriety as 'resting cells'.

3. Either toward the close of the mature stage or perhaps even before its commencement in some instances, secretions become elaborated which, aided by pressure due to the growth of the regenerative cells or to muscular contraction, result in the bulging of the cell contents entad. At this stage, the cells are known as old or secretory cells and are eventually sluffed off into the lumen, but the manner in which this process takes place varies all the way from a casting off of all the epithelial cells at once as in Hydrophilus (See Rengel, 1898) to a gradual removal and replacement of individual cells here and there. In the latter case, the cells may begin by giving off small quantities of their contents while the cuticular border is still present, but eventually this is cast off either freely or as fragments adhering to the margins of the globular masses of secretion. (See Van Gehuchten, 1890). But whether the process is slow or rapid, the end result is the discharge of the entire cell as a more or less large sphere of secretion containing a degenerating nucleus.

As regards the function of the mature cells, aside from

their significance as an intermediate stage in the secretory life cycle of the midintestinal epithelium, it will suffice to say that, in the light of the best experimental evidence, they are absorptive, and among the most thorough and conclusive treatments of this subject may be cited those of Cuénot (1898), Petrunkevitch (1900) and Sanford (1918). It will be seen that this interpretation partly if not wholly accounts for the presence of the cuticular border in this instance, since many cells which are purely secretory throughout their life cycles do not possess it, and it therefore can not be looked upon as indispensable to secretory activity. Thus the functions of digestion and absorption, instead of being assigned to two or more genetically independent types of cells as in Vertebrata, are here assigned to different stages in the life history of a single type.

Until quite recently, no very thorough or accurate studies have been made on the midintestinal epithelium of Diplopods. Plateau (1878), whose observations were based entirely on dissections, notes that the epithelial cells of Julus are loosely connected and possess, sometimes ameboid but usually club shaped tips containing yellowish green granules. He describes those of Glomeris as being larger and flatter than in the former but possessing the same kind of granular content. Visart (1895) was seemingly the first to describe the regenerative cells, but he claims that they divide by amitosis in contrast with the mature and old or discharging cells which undergo mitotic division. Also, it is not apparent that he recognized any genetic relationship between the regenerative and mature cells. Krug (1907), Effenberger (1909), Wernitzsch (1910) and Reinecke (1910) refer

to the epithelium as consisting only of columnar cells containing granules and, except in Julus, provided with a distinct cuticula, Krug, however, observes that the cells are always higher at the posterior extremity of the midgut than elsewhere. Léger and Duboscq (1904), in describing the epithelium of Julus, Craspedosoma and Polyxenus, were the first to view the cells from the standpoint of our present day interpretations regarding their interrelationship and functions in Arthropods as a whole. For Julus they depict the basement membrane as thick, structureless and distinctly corrugated, as opposed to Visart's contention that it is made up of connective tissue, and present the regenerative cells as diffuse, cone-like, broadly attached to the basement membrane and having nuclei distinctly smaller than those of the mature cells but with a more conspicuous karyosome. They also find that their reproduction is exclusively mitotic and are thus in accord with the prevailing view today. The mature cells are described as high and cylindrical, with a cuticular border consisting of a basilar membrane bearing a regular brush of dense hairs, and with elyptical nuclei situated either centrally or nearer the basement membrane. Basally the cytoplasm is quite homogeneous and takes a deep stain, but entad of the nucleus it is filled with regularly arranged, yellow spherules of secretion. On the way toward expulsion, the discharging cells are separated by constriction from the basement membrane, and have the appearance of pyriform bodies containing either a deeply and evenly stainable mucoid mass or yellow secretory granules. Within the old cells a nucleus may or may not be visible, but when visible shows distinct evidence of chromatolysis. It would appear that

Craspedosoma differs from Julus only in regard to the secretory granules of the mature cells which are shown as irregularly scattered but more abundant in their basal than in their ental parts, while in Polyxenus the chief difference lies in the extreme variability of the cells which are often columnar but tend to become flat and even syncytial, especially at moulting times. Verhoeff(1912 and 1914) describes the midintestinal epithelium of Julus and Polydesmus, but, aside from its behavior during ecdysis, has observed, insofar as I have been able to determine, very little which has not been brought out by Léger and Duboscq.

My own observations are fundamentally similar to those of Léger and Duboscq, but, because of their varied nature, it will be convenient to consider them under the following subheadings.

(a) Basement Membrane.

In all four genera the basement membrane appears structureless but distinctly thickened and directly continuous with the corresponding membranes of the oesophagus and hindintestine. It always stains a deep blue with Mallory and thus bears a closer resemblance to the chitinous intima of the other divisions of the tract than to the peritrophic membrane which takes a light blue stain, but, inasmuch as the secretion in the ducts of the posterior salivary glands of Parajulus and anal glands of female Scytonoti and Orthomorphae has a similar reaction to that of the basement membrane, one can find here no valid basis for regarding the latter as chitinous. Moreover it is non-resistant to potassium hydroxide as I have already pointed out, and when obliquely

sectioned it often presents a fibrous appearance. (See Fig. 23.) When the midgut is in its usual, moderately contracted condition, the membrane appears evenly and closely corrugated in both transverse and longitudinal planes, but becomes smooth and flat when the former is expanded. (See Fig. 28 A. and B.). In Fontaria, however, because of the tendency of the epithelium to become broadly undulated under contraction, this close corrugation is less pronounced. (See Figs. 24 to 48.)

(b) Regenerative Cells.

The regenerative cells, though always diffuse, show great variation in their abundance in different areas of the epithelium. Where the latter is low due to the expansion of the midgut, they are fewer within a given range than elsewhere (See Fig. 28 A and B.), and are more numerous at points where active secretion is going on than where the free margin of the epithelium is level and bears the cuticular border. In Parajulus, as in Julus, according to Krug (1907), they are always more abundant at the posterior extremity of the midgut than at other levels, thus giving the epithelium a thick, stratified appearance. (See Fig.50.). The nuclei of the very young cells are somewhat smaller than those of the latter stages and often show irregularities of shape which suggest amitosis. (See Fig. 34.), Otherwise they are quite similar to the nuclei of the older cells and appear clear with one or two central nucleoli under Flemming's fixation or with a distinct chromatin content under Bouin's. I have no reason to doubt that they divide by mitosis although I have seen only a few suggestions of mitotic figures. (See Figs. 29, 30 and 32).

As the cells grow toward the free margin of the epithelium, the nuclei very soon attain their full size and the cytoplasm, homogeneous at first, becomes very clear and finely reticular, while, as the first evidence of secretion, a few distinct granules can almost always be found within the cytoplasm. The shape which the cells assume during their period of growth is obviously dependent on the amount of pressure which they are obliged to resist and consequently varies all the way from fusiform to spherical, and when the very young cells are numerous the former may become constricted at their point of attachment to the basement membrane long before maturity is reached. (See Fig. 34). Because of the pronounced variation in number and shape due to constantly changing physiological conditions, it is difficult to recognize clear cut specific or generic differences in the regenerative cells, but I can say with assurance that, especially in regions where the cuticular border is present, they are fewer in Scytonotus and Orthomorpha than in the other genera, while in Fontaria they tend more toward the broad, rounded shape than in Parajulus. (See Figs. 28 to 41).

(c) Mature Cells.

In normal, actively feeding specimens, the distribution of the mature cells in the midgut at any one time seems to be largely dependent upon the amount and position of the solid food matter in the lumen. Because of the large amount of earth and pebbles which are always mixed with the latter, and often cause the entire loss of the lumen's contents in the sectioning process, I relied exclusively upon fresh dissections in reaching this con-

clusion. By immersing freshly removed intestines in distilled water, I had little difficulty in obtaining optical sectional views clear enough to enable me to distinguish between the mature and discharging cells. Then, upon carefully notice the position of the solid food masses, slitting open the intestine and removing everything within the lumen, I treated the midguts with osmic acid which stains the secretory granules an intense brown (See Nussbawn, 1877), and therefore sharply differentiates the old secreting cells from the remainder of the epithelium. In this way I found that whenever solid food matter completely filled the midgut, the discharging cells were far more numerous than the mature which were confined to limited areas here and there. On the other hand, when only two or three masses were present at wide intervals apart, the mature cells dominated over the discharging and occupied the intervals, while the latter were chiefly confined to the areas immediately adjacent to the solid food. Very rarely in the anterior intervals but quite commonly in the posterior, the mature cells were interrupted by small groups of the discharging, while, in Parajulus, the posterior extremity of the epithelium was always in a more or less active state of discharge. This might simply indicate that as the solid matter proceeds caudad in the midgut, more and more of its digestive content goes into solution, since it can hardly be presumed that the presence of solid matter whether digestible or indigestible could cause by purely mechanical means, the completion of the secretory process and the release of the enzymes. In one Parajulus midgut with only a single food mass which was situated at

its anterior end, the discharging cells seemed to be wholly confined to the anterior part of the tract, while the mature cells occupied the remainder. The epithelium of the posterior two thirds of the gut presented a smooth and even free margin, but at a point just caudad of the discharging cells, it appeared irregularly thickened and wavy and over these irregularities its cuticular border was distinctly narrower than elsewhere. It will be noted that this part of the epithelium had been a longer time without food matter in its immediate vicinity than any region posterior to it, and, as I shall shortly point out, this same condition can be apparently induced by starvation, and is, seemingly the concomitant result of the inhibition of the secretory tendancy and the proliferation of the regenerative cells, which seems to continue regardless of external factors. But without going any further into this matter at present, it may be concluded that the discharging cells are predisposed to be most numerous at levels of the epithelium adjacent to solid masses within the lumen, because digestible matter is more abundant in the vicinity of the latter than elsewhere, and that the absence of digestible matter tends toward the indefinite prolongation of the mature stage. The foregoing observations were made on ten Parajuli and two Orthomorphae and I therefore only assume that these condtions are applicable to the other genera as well.

When the midgut is in its normal state of contraction, the mature cells have an average height of about 40 microns in Parajulus, 32 in Scytonotus and Orthomorpha and 35 in Fontaria, but this may be reduced by one half or more in Parajulus when the lumen is distended. (See Fig. 28.A. and B.). The nuclei usually

occupy positions midway between the two ends of the cell but may sometimes be found at higher or lower levels than these. In Parajulus and Fontaria the basal parts of the cells are usually much more constricted than in the other genera where the regenerative are fewer. Anterior to the nucleus, a very uniform spongioplasmic reticulum can almost always be seen and in Parajulus this sometimes extends down into the basal part of the cells as well. (See Fig. 28 A.) Under Bouin's fixation, each mesh of the rectículum appears to contain a single large vacuole, while sometimes under Bouin's but almost always under Flemming's very distinct granules seem to supplant the latter (See Figs. 33 and 35). The basal parts of the cells are usually deeply and uniformly stained and especially so in Scytonotus and Orthomorpha. (See Figs. 30 and 31.).

In some of my preparations the cuticular or brush border has the appearance of a refractive, structureless membrane of even thickness, but more often its processes are clearly defined and much more suggestive of very symmetrical, slightly fusiform and closely apposed evaginations of protoplasm than of hair-like projections. Occasionally in Parajulus I have found them long, narrow and relatively far apart (See Fig. 28. C.), but never solid or rod-like, and usually showing the same staining reactions as the underlying cells. Characteristic basal thickenings may be clearly recognized in newly developed brush borders, where they seem widely separated from each other and connected with the spongioplasmic reticulum (See Fig. 34. B.B.F.), but elsewhere they are more or less contiguous and commonly form a deeply stained, uninterrupted basilar membrane. (See Figs. 28 to 34).

In Scytonotus and Orthomorpha the brush border is relatively thicker than in the other genera. (See Figs. 30 and 31).

Frequently the brush border is replaced along the periphery of the mature cells by a relatively dark staining, homogeneous matrix which connects at irregular intervals with strands of the peritrophic membrane or which, if followed anteriorly or posteriorly for some distance, is seen to gradually detach itself from the epithelium and continue as the peritrophic membrane itself. This indicates beyond question that the latter is secreted by the midintestinal epithelium, although, when Mallory's stain is used, the matrix appears as a distinct red band lying either below or above the basilar membrane of the brush border; while all parts of the peritrophic membrane within the lumen stain light blue. With mucicarmine, however, both matrix and membrane stain a uniform red and in so doing suggest not only a close interrelationship but also the possibility that both are mucoid as well as chitinous in composition. Sometimes the brush border processes are visible, especially where the matrix is just becoming detached from the cells.(See Fig. 23), and it may be reasonably assumed that their appearance marks the beginning or the close of this secretory activity. (See Figs. 24 to 28). Thus, assuming that the mature cells are absorptive, two additional functions must be ascribed to them; most of the earlier stages in the elaboration of the enzymes, and the secretion of the peritrophic membrane.

(d) Old or Discharging Cells.

In the senescence of the mature cells three processes are

clearly definable. In the first place, the bases of the cells become more and more constricted until reduced to mere thread-like attachments which eventually break. Occasionally, however, in Parajulus the distal parts rupture and discharge their contents before the basal parts are freed from their attachment to the basement membrane. (See Fig. 34, R.C.). Also in Scytonotus it would appear that they may often become detached from the latter without any pronounced constriction of their basal part. (See Fig. 38). But in all cases where the discharged cells have become constricted and broken away from their attachment they appear more or less balloon-like with a well rounded ental margin and a tapering basal projection. Often one and occasionally two nuclei may be seen within them, but I would explain the latter condition as a result of degeneration, since the cells, when freed from the epithelium, are dead, as evinced by the fact that both nuclei and cytoplasm are stained by ammonium carmine which in several instances I mixed with the Diplopod's food. (See Fig.34.). In the second place, the granules, conspicuous even in the mature cells, become larger and more numerous, while the spongioplasmic reticulum breaks down. (See Figs. 34 and 35). But in many instances, the latter are fully elaborated before the shape of the cells is materially altered, and the secretion may be discharged in small quantities previous to the definite discharge. (See Figs. 33, 38 and 39). Often no granular content seems to be present at all, but is replaced by clear vacuoles or a dark staining mass which is possibly mucoid, (See Fig. 38), while, under Bouin's fixation and haemalum, eosin, orange G. stain, the sluffed off masses are seen to be filled with refractive reddish vacuoles of more or

less even size. (See Fig. 36.). It must be noted, however, that in all the fresh material that I have examined, the old cells contained distinct greenish yellow granules, which turned brown with osmic acid. This reaction, according to Nussbawm (1877), indicates that they are zymotic, but more recent investigations have shown that osmic acid cannot be relied upon as an indicator in this respect. Whatever their physiological significance may be, I am inclined to regard the granules as the usual form which the elaborated secretion takes. They are somewhat larger and more distinct in Scytonotus and Orthomorpha than in the other genera (See Figs. 34 to 41). In the third place, the brush border is cast off during the earlier stages in the discharge of the secretion, which first becomes fully elaborated directly beneath the former and causes it to bulge out into the lumen. (See Fig. 33. A.). Finally, when the part of the cell or cells containing this secretion is discharged, the overlying brush border goes with it. (See Fig. 33. B.B. 2.). In more advanced stages of discharge, no vestiges of the old brush border may be found, though new ones formed by recently matured cells are often distinguishable. (See Fig. 34. B. B. F.). The height of the epilethium at times of discharge is obviously quite variable, but it may be said to average about 60 microns in Parajulus and 45 or 50 in Scytonotus, Orthomorpha and Fontaria.

(e) Effects of Starvation and Hibernation.

Having been impressed by the observations of Needham (1897) on the effects of inanition upon the midintestinal epithelium of dragonfly nymphs, I became desirous of determining how Diplopods

would react in this regard under similar conditions. Accordingly, in the early part of November, 1919, when the bulk of my stock specimens of Parajulus were beginning to hibernate, I isolated twelve individuals, mostly adult males and females, by placing them in a separate container partly filled with earth. Since I wished to keep them active and to counterfeit summer or early fall conditions as closely as possible, I exposed the container to room temperature and a moderate amount of sun light and maintained sufficient moisture inside by keeping the cheese cloth covering its mouth constantly wet. To prevent the specimens from feeding, I plugged their mouths with very thick damar, which quickly hardened when exposed to the air of the room, and repeated this operation at intervals frequent enough to assure me that no food was consumed during the experiment. At first I was in doubt as to whether the combined effects of moisture and digestive ferments would not soften the damar so that it could be rubbed off or swallowed, but I found no indications of either result, although the damar was usually soft enough to cause grains of sand and loam to adhere to it. This procedure at once raises the question as to why I did not resort to the commoner method of providing a sterile environment for the Parajuli. Without denying that such methods might prove effective, I can merely cite my previous unsuccessful attempts at keeping Parajuli alive for any length of time when not provided with a loamy substratum into which they could burrow. As a substitute for the latter, I often used moist sterile sand, but within a day or two the specimens invariably died. Thus, in view of the diversified organic matter which the Parajuli consume with large quantities of earth

and of the difficulty of maintaining sterility for a long period of time, I concluded that the control of the animal itself was both a surer and a simpler way. During the first few days of the experiment the specimens were quite noticeably inconvenienced by the damar and three of them died, but the remaining nine were soon able to crawl about with apparently as much ease as a normal animal and were active whenever I made my daily examinations.

After the Parajuli had starved for twenty days, I killed all of them and, upon grossly examining their digestive tracts, found no residual solid matter in the midguts and only a small amount in the hindguts of a few specimens. In their outward contour the midguts presented no unusual features and, consequently, no suggestion of pronounced circular constrictions at frequent intervals along their courses, such as Plateau (1878) observed in a Julus which he starved for fifteen days. Then I examined the epithelia in optical sectional view and finally treated the material with osmic acid, thus using the same method which I have already mentioned in reference to the normal mature cells. This brought to light the following conditions:

1. Old cells in the process of discharge were apparently absent from all parts of the epithelia except the posterior extremity and in three specimens they were lacking here as well.

2. The mature cells, therefore, lined all the remaining extent of the epithelium and, except in a few places where the gut was obviously distended, they presented the same wavy, irregularly thickened appearance which I previously mentioned as being confined to a very limited area in a normal specimen.

3. In the regions where the tract was distended, the mature cells presented an even free margin and a thicker, more prominent brush border.

4. The epithelium at the posterior end of the midgut, whether in the process of discharge or not, always showed a greater average thickness than was noticeable anywhere else, and a greater number of regenerative cells. In the three specimens where there was no indication of discharge as it normally appears, the cells bordering the lumen were much smaller and rounder than the corresponding mature cells of the anterior regions of the gut. They were also unattached to the basement membrane, could be readily freed from the epithelium by jarring the cover glass, and showed no vestiges of a brush border.

5. The regenerative cells which showed up quite clearly here and there were very numerous and densely massed at the points where the thickenings of the epithelia occurred, and consequently the basal parts of the mature cells appeared more constricted and attenuated than in the normal brush border epithelia.

Up to this point my observations were fundamentally in accord with Needham's on dragonfly nymphs, the most outstanding difference being the more regular disposition of the thickenings in the latter, which is probably due to the fact that the regenerative cells are clustered in evenly spaced nidi in Odonata and, irregularly diffuse in Diplopoda. But Needham further noted that the thickenings and foldings become more and more accentuated under continued starvation, while I, in comparing these modifications in the normal epithelium already mentioned with those in the starved, had observed no appreciable difference in

height but only a greatly increased distribution in the latter. With the hope of obtaining more definite information on this point, I next starved one adult male thirteen days, another eighteen, and an immature female forty two, using the same method as in the first experiment. Inasmuch as these individuals had already started to hibernate before I selected them, they were a longer time in becoming active through response to increased warmth and sunlight than my earlier specimens, but in other respects behaved similarly. Upon gross examination, the midguts of all three appeared essentially alike, except that the thirteen day male showed vestiges of solid matter a short distance anterior to the pyloric valve. In order to observe whatever differences might obtain with as much accuracy as possible, I made almost complete serial sections of the entire tracts, and, as a result, found dissimilarities but not altogether as I had anticipated.

1. The epithelium of the thirteen day male was entirely in the brush border stage, except for one or two very limited secretory areas, but throughout the anterior nine-tenths of the gut it appeared perfectly normal, with a height of from 40 to 50 microns, and without any distinct folds or thickenings. Posterior to this, however, it showed the characteristic wavy contour, reduced brush border and increased number of regenerative cells beneath the folds which averaged 90 microns in height. In many places the basal parts of the mature cells appeared so constricted that I was unable to trace their connections with the basement membrane, while their cytoplasm was very similar to that of the regenerative cells and suggested either degeneration

or retarded development. (See Fig. 42). At the posterior extremity of the midgut, the epithelium presented an appearance quite different from anything observed in my other starvation and hibernation specimens. Here its thickness was increased to 95 or even 105 microns and the regenerative cells were extremely abundant which is not unusual, but entad of the latter, were five or six tiers of elongated cells much smaller than ordinary mature cells and with their long axes tangential rather than radial. They thus resembled a stratified squamous epithelium, were disposed in more or less regular folds about the lumen and, though detached from the basement membrane, were bounded peripherally by a very vestigial cuticular border (See Fig. 41.) In cross sections near the pyloric valves of two normal specimens, I have observed a similar stratification of elongated cells forming an almost complete ring, but in these instances there was a complete detachment from the epithelium which was in the usual active state of discharge. In every case, however, the cytoplasm took quite a dark even stain which suggested a histolytic condition and which I am inclined to associate with the old epithelial cells cast off during ecdysis, such as Verhoeff has described in Julus (1912) and Polydesmus (1914). Since, however, I observed nothing else in any of my specimens which I could attribute to moulting I am unable to further substantiate this view.

2. In the eighteen day male, the epithelium of the anterior nine tenths of the gut was distinctly thickened and wavy in outline, except in a few places where the lumen was distended and the cells low and even. There was thus a very close similarity to the corresponding epithelia of the twenty day specimens which

I examined fresh, but the cytoplasm of the mature cells was more normal than in the thickened areas of the thirteen day male and did not exceed 70 microns in height. A very few remnants of old cells could still be seen here and there, while, as in six of the specimens examined before, the posterior region of the gut was in an active state of discharge and from 80 to 100 microns in thickness. It will therefore be observed that in the anterior nine tenths of the gut, the eighteen day specimen showed a wider departure from the normal than the thirteen day, while in the posterior tenth the reverse was true.

3. I was surprised to find that the forty two day female differed from the preceding specimen only in respect to the posterior extremity of the epithelium which showed no indications of normal discharge and closely resembled this region in the three twenty day specimens where the ental margin was lined by an aggregation of closely apposed but easily dissociated, small, rounded cells. But here the epithelium could be studied in greater detail than in the other specimens, and was seen to be disposed in quite symmetrical thickenings which projected well into the lumen and averaged about 80 microns in height. The summits of the thickenings were occupied by the small cells which were always clearly marked off from the densely massed regenerative cells below them and presented an evenly vacuolated cytoplasm together with a deeply stained, picnotic nucleus. Some of the cells were detached from their respective clusters and free in the lumen, while at the base of the depressions separating the groups a very shallow brush border was often discernible. (See Figs. 43 and 44). My present data are too limited to en-

able me to definitely correlate these rounded, vacuolated cells with the flat evenly stained cells of the thirteen day male. Their positions are obviously analogous and there is little doubt that both represent end products on the way toward expulsion. The best explanation which I can now offer is, that they are old cells in which the secretory process has been more or less inhibited but in which the detachment from the basement membrane has been effected in the normal way by the regenerative cells. Their accumulation in large numbers might be explained by the persistence of the cuticular border which I have already noted as being present in a very reduced condition, while their difference in shape in the two specimens might be due to the border's greater or longer resistance against centripedal pressure in the case of the flat cells than in the case of the round. At all events, a cuticular border is definable along the entire periphery of the lumen in the thirteen day male, but noticeable only in the depressed intervals between the clusters of round cells in the forty two day female. (See Figs. 41 and 44.).

A comparison of the three specimens starved for varying lengths of time shows a successive decrease in the number of normal old cells, a tendency for the eipthelium to become locally thickened and wavy in outline over increasingly greater areas, but no accentuation of these thickenings and irregularities which might be correlated with the length of the periods of inanition. The fact that the epithelia of Needham's (1897), dragonfly nymphs increased steadily in thickness during two months of starvation, which was the time limit of his experiments, might suggest a

variation in different Arthropods of the potentiality of the regenerative cells to reproduce and grow without replacing discharged cells. But it is more likely that such potentialities would vary more with the seasons than with species or genera, and out of regard for this assumption, I am inclined to ascribe the failure of the Parajulus epithelium in showing a continuous series of changes to the fact that my experiments were conducted in the winter. Moreover, it is doubtful that the warmth, sunlight and outward activity of the animals in crawling about, could have gone very far toward modifying any deep seated laws controlling the seasonal behavior of the regenerative cells.

In order to compare the results so far obtained with conditions under hibernation, I selected twenty Parajuli which had been hibernating about two months and examined their midguts fresh by the same method which I used for the twenty day starvation specimens. None of them seemed to have any solid matter in the midintestinal lumen but in four specimens, the hindgut appeared quite well filled. The epithelia in the anterior nine tenths of the gut were all very much alike and indistinguishable from those of the twenty day Parajuli. But it is interesting to note that the posterior tenth of the epithelia was in an active state of discharge in the four specimens with solid matter in their hindguts, while in the remaining sixteen, it presented the same clusters of rounded cells which I observed in the forty two day female and three of the twenty day specimens.

Having made these observations, I next selected an adult hibernating female which I allowed to become active and in the course of a day succeeded in getting her to eat a small quantity

of banana and apple mixed with ammonium carmine. Two days later I killed her and, after examining her midgut which plainly showed the carmine within its lumen, made serial sections which brought out fundamentally the same conditions observed in the forty two day female but intensified in some respects. In the anterior two thirds of the gut similar thickenings and surface irregularities were noticeable as well as a few areas where the lumen was expanded and the epithelium low and even. But in the posterior third, the thickenings increased their height from 65 to 100 microns and resolved themselves into evenly spaced, symmetrically rounded eminences which jutted well into the lumen. (See Fig.45). Here the cytoplasm of the mature cells was very similar in character to that of the regenerative cells, thus recalling the condition referred to in connection with the thirteen day male. (See Fig. 42.). The epithelium at the posterior extremity of the gut was very much like that of the forty two day female, but with its greater relative thickness of 120 microns, it nearly effected a complete closure of the lumen. Here a few of the small rounded cells which were detached from the epithelium had both nucleus and cytoplasm stained red by the carmine, thus showing that, like the normal old cells which react similarly to the vital stain, they are dead or dying products. Inasmuch as the old cells were very few and widely scattered within the anterior two thirds of the epithelium, it is probable that they were merely undiscarded remnants and had nothing to do with the food recently consumed. Furthermore, it is obvious that the epithelium remained unresponsive to the latter which was eaten two days before the animal was killed. This contrasts markedly with Needham's dragonfly

nymphs which were fed after two months starvation; for in this instance the mature cells immediately underwent senescence and were sluffed off in enormous numbers as the food matter traversed the midgut. It also suggests that in Parajulus the epithelium is more responsive to seasonal tendencies than to food within the gut when the two are in opposition.

It will be seen that the epithelium is both the starved and hibernating specimens presented essentially the same conditions and it would be reasonable to assume from this that starvation and hibernation bring into play the same set of tendencies and therefore give rise to the same modifications in the midintestinal epithelium of Parajulus. It might, however, be objected that, because my starvation experiments were conducted at a time when the Parajuli were normally hibernating, my 'starved specimens' did not show the effects of starvation but only those of hibernation. I can answer this objection only by citing Needham's results which indicate similar tendencies on the part of the epithelial cells and are ascribed to starvation alone. Nevertheless it must be noted that Needham's experiments, like my own were conducted during the fall and winter months. But, without regard as to whether one or both were the factors involved, I am fully justified in concluding that when the Parajuli stop feeding the mature cells tend to remain indefinitely in the brush border stage, while the regenerative cells by continued proliferation and growth cause a basal construction of the former which results in an unequal increase in their height and thus gives rise to the marginal irregularities of the epithelium.

(b) Gregarine Parasites.

I shall close my account of the midintestinal epithelium with a description of some Gregarine parasites which I found quite abundant in Parajulus and Fontaria. The form occurring in Parajulus appeared most commonly in its intracellular sporozoite and trophozoite stages but was not at all rare in its mature trophozoite stage which is free within the lumen. The intracellular sporozoites were usually situated in the middle or basal parts of the mature epithelial cells which they infested and in their size and irregularly fusiform shape suggested small regenerative cells, but were always distinguishable by their deeply stained, homogeneous cytoplasm, their clear large nuclei containing a prominent central karyosome, and a distinct clear space separating their periphery from the cytoplasm of the host cells. In the intracellular trophozoite stage, which is characterized by the differentiation of the cell body into two clearly separable regions, protomerite and deutomerite, two distinct types could be recognized; a rounded one almost as broad as long and a more or less elongated one always having a length exceeding one half of its breadth. In both forms the protomerite is ectad in position which, according to Léger and Duboscq (1904), is normal for intracellular Polycystid Gregarines though not without exceptions. Many of my preparations showed individuals of this stage in sizes renging from a length of 20 to 40 microns and indicative of different periods of growth. In the former the cytoplasm was dark and even like that of the sporozoites, while in the latter it had become finely retcular or granular as it is typically found in the mature stage. It could also be clearly

demonstrated that as the trophozoites grew large they became pushed more and more toward the free margin of the epithelium thus passively yielding to the pressure of the regenerative tissue like the cytoplasm of their mature host cells and, at the same time, causing a tremendous expansion of the latter in their distal parts and a jutting of the brush border well out into the lumen. (See Fig. 46 A.). The mature trophozoites varied somewhat in the relations of width to length and from a length of 130 to 235 microns, but all that I clearly observed were of the more elongated type. The nucleus with its prominent karyosome was always centrally situated in the deutomerite, while the protomerite was more or less pointed anteriorly but broad posteriorly and often showed a few very dark granular bodies in its cytoplasm. At the anterior extremity of the protomerite a distinct medial pore could usually be seen penetrating the epicyte or outer pellicle of the Gregarine, but its presence or absence was obviously due to the sectioning planes. (See Fig. 46 B.).

The mature trophozoite stage of this Gregarine corresponded so closely in all the characters which I could determine to those of Stenophora julipusilli-Leidy, which Crawley (1903) found in the midintestinal lumens of a great number of American Juli and Parajuli, that I can hardly doubt its identity with the latter. Although Crawley has evidently not seen the intracellular stages of this species, Léger and Duboscq (1904) have carefully observed them in the very closely related Stenophora juli-Frantzus and their observations are very similar to my own. It will be noted that the cephalont or epimerite stage is apparently lacking in both species, but Crawley, while admitting that this is true as

regards Stenophora juli, considers the pore of the protomerite in the mature Stenophora julipusilli as the rudiment of an epimerite. The cysts and sporocysts have not been observed in the latter species but they are probably not unlike those of Stenophora juli as described by Léger and Duboscq.

Crawley also found a Gregarine in some American species of Polydesmus and Fontaria which he named Amphoroides fontaria, but which he describes as very similar to Stenophora and lacking an epimerite. I have seen no parasites resembling this species in my specimens of Fontaria. In one of the latter, however, I observed the mature or nearly mature trophozoites of a form possessing a blunt epimerite as wide as the succeeding protomerite but usually longer and thus recalling Stylorhynchus and other Gregarines infesting insects (See Léger and Duboscq, 1904). In length they averaged about 100 microns and their deutomerites were dilated in their mid region but usually ended posteriorly in more or less acute points. The nuclei, together with their central karyosomes, were very distinct, while the cytoplasm was finely and evenly reticular as in Stenophora. Most of the individuals were free in the lumen, but in a few instances I found them still attached to the epithelium and with their epimerites penetrating well into the host cells and lying to one side of the nucleus. (See Fig. 47, A and B.).

(c) Muscularis.

All of the Diplopods so far investigated are alike in possessing a midintestinal muscularis consisting of inner circular and outer longitudinal fibers, and Effenberger (1909), Wernitzsch

(1910) and Reinecke (1910) are virtually agreed that both layers are closely apposed to each other and that the fibers of each are similar but of distinctly smaller caliber than the oesophageal or hindintestinal muscles. Effenberger and Reinecke, however, observe that the longitudinals of Polydesmus and Polyxemus are quite few and irregularly distributed. Krug (1907), while recognizing the circular fibers of Julus as small and evenly distributed finds that the longitudinals are larger, tend to become gathered in irregular groups toward the anterior end of the midgut and interconnect at various points with the circular. Léger and Duboscq (1904) also show the longitudinal fibers of Julus as larger and occurring in groups, but figure and describe them as lying ectad of a layer of cells which bounds the entire midgut peripherally in most Diplopods and which will claim my attention very shortly. It will be seen that Krug and Léger and Duboscq are disagreed as regards the position of the longitudinal layer in Julus and since the former based his results on Julus Mediterraneus and the latter on Julus albipes, it may be reasonably assumed that the position of this layer varies specifically within the genus. Authorities are unanimous in recognizing both sets of fibers as striated.

In Parajulus, Scytonotus and Orthomorpha the muscularis is very much alike and limited throughout to the narrow space between the basement membrane of the epithelium and the peripheral layer of cells mentioned in the last paragraph. The fibers of both layers are of very small and even diameter and spaced with almost mathematical regularity, though the intervals separating them vary with contraction and expansion. Throughout their ex-

tent in the midgut, I have seen no indication of collateral branching and when seen in surface view they form an even net work with only a few diffuse connective tissue cells or processes spanning the square meshes between them. (See Fig. 48). The longitudinal fibers which number about 140 to the cross section at all levels of the midgut, unite with each other in the regions of the cardiac and pyloric valves and thus give rise to larger but fewer fibers which become the outer oesophageal longitudinals on the one hand and the hindintestinal longitudinals on the other. I have no reason for doubting that both sets of muscles are striated, although I have seen only slight traces of this condition. (See Figs. 28 to 32).

The muscularis of Fontaria answers to the above description in all respects but two which relate to the longitudinal muscle fibers. In the first place, the latter number about 220 to the cross section rather than 140, and in the second place, they are not merely the anterior continuations of the hindintestinal longitudinals but arise as small, secondary branches from them. At a level just caudad of the pyloric valve, the longitudinal fibers of the hindgut are disposed in about twenty five or thirty evenly spaced bundles, each comprising a similar number of fibers. From this point the bundles continue cephalad over the peripheral cells of the midgut, thus recalling the position of the longitudinals which Léger and Duboscq noted in Julus albipes. Some of the former end a short distance anterior to the pyloric valve, while from fifteen to eighteen reach within one or two millimeters of the cardiac valve, but gradually lose their fibers and become smaller in their course forward. They may thus be re-

ferred to as the outer midintestinal longitudinals as opposed to the much smaller inner longitudinals which lie beneath the peripheral cells and, as I have already intimated, originate from the former a short distance cephalad of the pyloric valve as branches passing obliquely entad to a level immediately above the circular fibers. Some distance back, I referred to the possibility of the midgut of Fontaria to become greatly and abruptly expanded at one point near its anterior end and another near its posterior, and it is highly probable that these outer longitudinal fibers constitute a special modification of the muscularis for effecting these expansions. (See Figs. 32 and 52).

D. Epitheloid Cells.

Ectad of the muscularis and covering the entire surface of the midgut is an epithelium, present in most of the Diplopods that have been investigated and composed of more or less cuboidal cells with dome-shaped outer margins and large central nuclei, invested by a vacuolated cytoplasm containing refractive yellow granules. This layer was first recognized in Julus by Plateau (1878) who rather vaguely refers to it as adipose tissue surrounding the midgut. Visart (1895) describes it in more detail but still regards it as adipose tissue. Rossi (1902) denies that it bears any relationship to fat but has no alternative theory to suggest. Berlese (1901) has nothing to say as to its function, but claims that its cells originate in common with the regenerative cells of the digestive epithelium as free wandering elements from the body cavity which eventually find attachment along

the wall of the midgut. He refers to them as external splanchnocytes and attempts to homologize them with the more irregularly massed cells which form the outer layer of the midguts of Crustaceans and Arachnids. Krug (1907) regards the layer as glandular, though he admits his inability to find ducts leading from it to the midintestinal lumen. Effenberger (1909) claims that it is entirely lacking in Polydesmus, but Verhoeff (1914), while not referring to it specifically, suggests that the former's observations on the midgut were based on specimens undergoing ecdysis and are thus inapplicable to Polydesmus in its usual condition. This, together with its presence in the Polydesmoids, Scytonotus, Orthomorpha and Fontaria upon every occasion that I have looked for it, would imply that the layer is normally present in Polydesmus but may undergo degeneration during ecdysis. Reinecke (1910) finds it lacking in Polyxenus, but describes a pair of botryoidal 'thoracid glands' laterally investing the anterior fourth of the midgut and comprising alveoli with small lumens and a columnar epithelium in which the nuclei are peripherally situated. He found the main ducts of these glands but was unable to trace them to their outlets. Wernitszch (1910) finds that it is present in Craspedosoma and very similar to that of Julus, but, without stating why, refers to it as the 'hepatic layer', presumably because of its analogy to the splanchnic chlorogogen layer of Annelids. Finally, Léger and Duboscq (1904) identified its elements in Julus as the end cells of the numerous and richly branched tracheae which invest the outer surface of the Diplopod midgut, and further suggest that the refractive yellow granules

may have some affinities with uric acid. It will be seen that the significance of this layer is very imperfectly known, and for this reason I shall refer to it simply as the epitheloid layer.

In Parajulus, Scytonotus and Orthomorpha, the epitheloid layers are similar and so much like those of Julus and Craspedosoma that it will not be necessary to describe them in much detail. Under ordinary conditions they may be referred to as cuboidal, often slightly columnar, cells with an average thickness of about 8 microns in Parajulus and 5 or 6 in Scytonotus and Orthomorpha, but can be easily reduced to a greatly flattened state by muscular expansion. (See Fig. 28 A. and B.). Usually they are of uniform size and shape and in close apposition with only occasional gaps, containing tracheae or connective tissue, separating them. The nuclei are centrally situated, round or oval and provided with a rather diffuse, lightly stained chromatin content, while the cytoplasm is always more or less vacuolated. Though varying numerically in different cells, the yellow, crystalloid granules are of constant occurrence, even size and most abundant near the nuclei. In sixth instar Orthomorphae as well as immature, 14 mm. Parajuli, they are apparently as distinct and numerous as in adults, and I can therefore offer no positive evidence that they accumulate with age like the uric acid crystals and urates of the outer fat bodies of insects which their appearance suggests. As regards the interrelationship between the epitheloid cells and midintestinal tracheae, my observations on Parajulus bear out those of Léger and Duboscq on Julus, since in a number of my preparations I have seen tracheoles

ending blindly close to one side of the former's nuclei and have sometimes distinguished intracellular peritracheal nuclei. (See Fig. 49). In the other genera, I have been unable to trace such clearly defined interconnections, but have no reason to doubt that the same conditions obtain. (See Figs. 28 to 41.).

The structure of the epitheloid cells of Fontaria shows quite as marked a deviation from that of the other genera as the muscularis. Here, instead of a compact epithelium of cuboidal, ectally rounded cells, is to be found a comparatively loose aggregation of elongated, spindle-shaped elements, which averages between 40 and 80 microns in thickness. Many of these cells are broad basally and show the clear, well rounded nuclei lying quite close to the basal level, while others, irregularly distributed among the former, have narrow stalk-like basal attachments which result in the elevation of the nuclei to higher levels. Thus, in regions where the cells are most densely massed, a stratified epithelium with nuclei in two or three places is well simulated. The yellow granules are mostly confined to the cytoplasm above the nuclei and are always limited to the expanded parts of the cells. Distally, the elements are more or less widely separated, and narrow down to thread-like processes that attach at an oblique angle to an outer cellular membrane which is continuous over the entire surface of the midgut and suggests a visceral peritoneum. But, aside from questions of homology, its importance as a means of attachment for the outer longitudinal muscle fibers which lie along its ectal surface, as well as a protection to the underlying epitheloid cells, is at once obvious. Moreover, its absence in the other genera which lack

outer longitudinal fibers, would indicate that it has very marked embryological significance. (See Figs. 27, 32 and 40).

E. Summary.

1. The peritrophic membrane is prominent in all four genera, largely chitinous in composition, and secreted by the mature gastric epithelial cells of the midintestine.

2. The basement membrane of the gastric epithelium is thick, non-cellular, more or less fibrous and, except under muscular expansion, presents a corrugated appearance which is less marked in Fontaria than in the other genera. Though staining like chitin under Mallory, it is probably non-chitinous or chitinous only to a very limited extent.

3. The regenerative cells are diffusely distributed, more in evidence where discharge is taking place than elsewhere, and probably more numerous in Parajulus and Fontaria than in Scytonotus and Orthomorpha.

4. The brush border processes of the mature cells suggest uniform, closely apposed, cytoplasmic evaginations rather than rod-like projections. Basal thickenings are often distinct but are usually so close together that they form a continuous basilar membrane.

5. The earlier processes in the elaboration of secretion are carried on by the cells in their mature stage, and the secretion when examined in fresh material, always takes the form of prominent greenish-yellow granules.

6. When the secretion is fully elaborated, the cells lose their brush border and may be then referred to as old. At first,

discharge may take place in small quantities but eventually the entire cells are discharged together with their nuclei, and are then replaced by regenerative cells which become mature by developing a brush border.

7. Prolonged absence of food matter from the midgut of Parajulus causes more or less irregular thickenings of the epithelium which give the margin of the lumen a wavy contour and are attended by a reduction in the thickness of the brush border. These thickenings are caused by the inhibition of the tendency toward senescence and discharge on the part of the mature cells, coupled with continued reproduction and growth on the part of the regenerative cells.

8. The epithelium near the posterior end of the midgut responds somewhat differently to these conditions than elsewhere and gives rise to separate clumps of round cells or to an uninterrupted stratification of flat cells bordering the lumen.

9. These modifications are the effects of hibernation and probably of starvation also, but since my starvation experiments were conducted at a time of year when the Parajuli are normally hibernating, hibernation alone may have been effectual.

10. The Polycystid Gregarine, Stenophora julipusilli-Leidy is a common parasite of the midintestinal epithelium of Parajulus venustus, and an unidentified Gregarine with a broad blunt epimerite parasitizes the same tissue in Fontaria virginiensis brunnea.

11. The midintestinal muscularis of Parajulus, Scytonotus and Orthomorpha consists of small evenly spaced inner circular and

outer longitudinal fibers which are probably striated. Fontaria, in addition to these layers, possesses bundles of larger longitudinals, which do not extend as far forward as the cardiac valve and are attached to a tough, cellular membrane enveloping the midgut ectad of the epitheloid cells. It is probable that these fibers are chiefly instrumental in effecting the great anterior and posterior expansions which characterize the midgut in this species

12. The epitheloid layer is well developed in all four genera and the yellow refractive granules prominent, but in Parajulus, Scytonotus and Orthomorpha the cells are cuboidal and closely apposed while in Fontaria they are long, fusiform and quite loosely organized.

13. In Parajulus and probably the other genera as well, the elements of the epitheloid layer serve as end cells of the mid-intestinal tracheae.

4. Hindgut.

As I have previously intimated, the hindgut is divisible into only two clearly defined parts; intestine and rectum. In using the term, intestine, which is commonly applied in a rather loose way to various divisions of the digestive tube, it must be remembered that I shall be referring exclusively to that part of the tract which lies between midgut and rectum. It must also be noted that I consider the two terms, hindgut and hindintestine, as having the same extension, and shall therefore use them interchangeably.

A. Intestine.

The intestine presents a greater diversity of structure in the Diplopods so far investigated than any of the remaining divisions of the tract, and from the standpoint of their gross anatomy alone, three type forms are clearly recognizable; straight intestines with the Malpighian tubules opening just cephalad of the pyloric valve, intestines describing a complete loop in their course to the rectum but similar to the first type in other respects, and straight intestines with the Malpighian tubules opening at a considerable distance caudad of the pyloric valve. To the first type belong those of Polyxenus, Craspedosoma and Julus, and, in the light of the combined observations of Reinecke (1910), Wernitzsch (1910), Krug (1907) and Plateau (1878), it would appear that the Polyxenus intestine is the simplest of the three, since, under ordinary conditions, its diameter is relatively uniform throughout and decreases so gradually caudad that no distinct regions are marked off. In Craspedosoma, however, it is clearly divisible into a straight, expanded anterior portion which comprises about two thirds of its entire length and a constricted posterior one, which arches slightly dorsad before uniting with the rectum. The condition in Julus is much like that of Craspedosoma but evidently varies somewhat specifically, since for J. terrestris, J. sabulosus and J. Londinensis Plateau recognized only the two divisions already mentioned while in J. Mediterraneus, Krug found that the anterior portion was secondarily divided into two parts by a constriction which marked the location of a well developed sphincter muscle. Plateau

further observed certain individuals of Julus terrestris in which the posterior portion was so strongly arched dorsad that it took the form of a loop. As a representative of the second type, the intestine of Glomeris marginata so far stands alone, but since both Brandt (1837) and Plateau (1878) describe the loop as occurring in a dorso-ventral plane, this condition might be regarded as simply a further modification of the arching or looping which is confined to the constricted posterior portion in Julus and Craspedosoma. The differentiation into expanded anterior and constricted posterior regions is here about the same as in Craspedosoma. In Polydesmus is to be found the only example of the third type which, within my knowledge, has been described up to the present time. Here three regions are clearly defineable and of these the anterior is equal to about a fourth or a fifth of the hindgut's entire length and limited posteriorly by the openings of the Malpighian tubules. The middle region is somewhat more expanded than the former and about three times as long, while the posterior is very short and constricted. This description is based chiefly on Effenberger's (1909) observations on Polydesmus complanatus but applies equally well to Verhoeff's (1914) somewhat diagrammatic representation of the hindgut of Polydesmus monticolus valicolus-Verh , in which he refers to the region anterior to the openings of the Malpighian tubules as the 'urinary chamber'.

The intestine of Parajulus belongs to the first type and corresponds very closely to that of Craspedosoma, but, while the anterior and posterior regions are always distinguishable, the

distinction is much more marked when the former contains faecal matter, which is usually situated well caudad. In no instances have I observed any appreciable quantity of the latter in the posterior region. (See Fig. 1.). The three Polydesmoid genera are all representatives of the third type and their intestines are thus similar to that of Polydesmus in all external respects. In Fontaria, however, the middle region shows a proportionally greater expansion than in the other genera and this, at times, may almost equal the anterior and posterior expansions of the midgut. (See Figs. 2, 3 and 4.).

(a) Pyloric Valve.

The pyloric valve in Diplopods has essentially the same plan of structure as the cardiac and consequently results from a more or less pronounced jutting of the anterior extremity of the hindgut into the posterior of the midgut. In Polyxenus, according to Reinecke's description and figure, it is apparently present in its simplest form and consists in an abrupt transition from columnar midintestinal to cuboidal hindintestinal cells which gradually become longer and more columnar posteriorly. The chitinous intima of the hindgut is shown as smooth and of even thickness, and it probably commences with the cuboidal cells, though in Reinecke's drawing it cannot be distinguished from the cuticular border of the midintestinal epithelium. Both the midintestinal and hindintestinal cells seem to take part in the bluntly rounded valvular inflexion and a well defined sphincter of two or three layers of circular fibers overlaps their point

of transition. In Polydesmus, as shown by Effenberger, there is a very distinct intermediate zone of cuboidal elements that abruptly yields to columnar midintestinal cells anteriorly and columnar hindintestinal posteriorly, and thus forms a sharp indentation of the intestinal wall which is continuous all the way around. Here the intima is shown as having an almost imperceptible beginning along the free margins of the intermediate cells, but no indications of a sphincter or valvular inflexions are shown. The pyloric valve of Craspedosoma is more complex. As in Polydesmus, there is an intermediate zone of small cuboidal cells and a similar abrupt indentation, but immediately posterior to this, a large, bluntly rounded eminence comprising densely massed round cells with very small nuclei interrupts the continuation of the cuboidal cells with the remainder of the intestinal epithelium. Wernitszch refers to this structure as the 'connective tissue ring' and considers its elements as simply densely massed connective tissue cells. It must be noted, however, that the latter are entad of the basement membrane and directly continuous with the epithelium both anteriorly and posteriorly. At the caudal side of this eminence, the intestinal epithelium is resumed as columnar cells which suddenly narrow down to cuboidal and, as suddenly, elevate themselves into columnar once more, thus forming a posterior indentation similar to the anterior one which separates the midintestinal epithelium from the 'connective tissue ring'. Just caudad of this posterior indentation, Wernitszch shows a fairly prominent sphincter overlying the epithelium, while the chitinous intima is represented as a simple, even layer beginning at the intermediate zone and continuing over the ental margin of the 'con-

nective tissue ring' and posterior indentation. In Julus Mediterraneus, Krug observed a condition quite like that of Craspedosoma but differing in three important respects; the intestinal epithelium is continuous over the ental margin of the 'connective tissue ring' as a cuboidal layer for the first half and a columnar for the second half of this distance, the cells of the 'ring' are shown as lying ectad rather than entad of the basement membrane, and the intestinal intima at the apex of the latter presents a great local thickening which bears several rows of tooth-like projections. Plateau (1878) found thirteen rows of anàlogous projections in Julus sabulosus which were spatulate rather than dentate. Krug regards this thickening of the intima and its teeth as a device which simply furthers the ordinary function of the pyloric valve in preventing the regurgitation of food matter from the hindgut into the midgut. He figures only a weakly defined sphincter which overlies the intermediate zone just anterior to the 'connective tissue ring'.

In Parajulus the structure of the pyloric valve approaches that of Craspedosoma much more closely than any of the other genera above described, but here the intestinal epithelium continues farther cephalad along the ental margin of the so-called 'connective tissue ring', as a much thinner but still columnar layer, and there is no suggestion of an indentation or cuboidal cells posterior to this. As in Craspedosoma, however, the cells of the 'ring' seem to interrupt the continuity between the intermediate cells and the remainder of the intestinal epithelium. At the anterior extremity of the intermediate layer the cells which, farther caudad, are distinctly columnar with large oval nuclei

and a fairly dark staining cytoplasm, become cuboidal and finally flat, lose their cell boundaries and show light, clear cytoplasm in which very few nuclei can be seen. This, like the small oesophageal cells at the junction of the midintestinal and oesophageal epithelia, is very suggestive of the proctodeal imaginal rings described and figured by Kowalevsky (1887) and Verson(1898), and may therefore be a regenerative center of the intestinal epithelium. (See Figs. 20 and 50). The so-called 'connective tissue ring', when viewed in cross section, as it possibly was not by Wernitszch and Krug in Craspedosoma and Julus, hardly resembles a ring at all but takes the form of six symmetrical, bluntly rounded cellular masses averaging about 130 microns in height and almost completely separated from each other by deep clefts. These pyloric eminences, as I shall call them, mark the anterior extremities of the six longitudinal rugae, and contrast noticeably with cross sections through the intermediate epithelium just ahead of them, which presents a relatively even height of 10 or 15 microns throughout its circumference. The cells composing the pyloric eminences in Parajulus have large, elyptical nuclei, diffuse cytoplasm and present an arrangement which suggests that they are all attached to the basement membrane but extend entad for variable distances like the regenerative cells of the midgut. That they do not all reach the lumen might be inferred from the position of their nuclei at varying levels in all planes of section, though it is doubtful if the entire limits of any of the cells were included in any one of my sections. From the basement membrane at more or less regular

intervals along its course over this structure, groups of fibers extend entad and attach to the bases of the low columnar marginal cells which are continuous caudad with the intestinal epithelium, thus giving the latter a firm support and indicating that the tissue does not constitute a true stratified epithelium. The chitinous, intestinal intima has an almost imperceptible beginning along the free margin of the intermediate cells, but is very distinct where it borders the pyloric eminences and presents prominent, closely set pore-like structures. Inasmuch as the cells of the eminences are entad of the basement membrane and stand in such close relationship to the intestinal epithelium, it is more reasonable to regard them as modified epithelial cells than as connective tissue derivatives. It is also probable that Krug was wrong in representing them as peripheral to the basement membrane in Julus, since both Wernitzsch's and my own observations are at variance with this interpretation.

The apparently porous intima in Parajulus would suggest a possible glandular or absorptive function for the cells underlying them. As in Craspedosoma, the intestinal circular fibers form a fairly well defined sphincter immediately caudad of the pyloric eminences. (See Fig. 50).

In Scytonotus, Orthomorpha and Fontaria, the pyloric valves are essentially similar and more like that of Polydesmus than any of the other genera that I have mentioned, but the intestinal epithelium does not become very noticeably lower at its junction with the midintestinal and the valvular infoldings, hardly definable at all in Effenberger's figures, are always more or less pronounced. The latter, though varying from 30 to 100 microns

in length in accordance with the contraction or expansion of the longitudinal muscles, are proportionally smaller and much more regular in Scytonotus and Orthomorpha than in Fontaria, and appear in cross section as almost symmetrical rugae from twenty four to twenty eight in number. In Fontaria they are extremely irregular and in longitudinal section are seen to present a variable number of secondary folds projecting from them at uneven intervals, but my material was insufficient for enabling me to determine their number to the cross section. As in Parajulus, the chitinous intima in these genera is simple in the region of the pyloric valve and begins at the point of junction of the two epithelia, but shows no indication of pores. Like Polydesmus, Scytonotus and Orthomorpha lack pyloric sphincters, but there is quite a prominent one in Fontaria overlying the valvular infoldings. (See Figs. 51 and 52).

(b) Intima.

Posterior to the pyloric valve, the intestinal intima has been described as a simple, chitinous layer of quite even thickness throughout its course to the rectum in all the Diplopods so far investigated, except Polydesmus regarding which Effenberger refers to even rows of posteriorly projecting teeth confined to the anterior region of the gut and beginning a short distance caudad of the valve. All the authorities agree that the intima is disposed in rugae but their statements are so general that it is impossible for me to adequately compare the disposition of the latter in the different genera. Both Krug and Wernitszch mention

six rugae for Julus and Craspedosoma which become more pronounced in the constricted posterior region of the intestine and which are always more irregular than the oesophageal rugae. Reinecke refers to the lumen of Polyxemus as star-shaped, but describes this as due to the unequal height of the epithelial cells and therefore not representing true rugae. Effenberger implies that no marked suggestions of the latter could be observed in Polydesmus.

In Parajulus, the intima has a much simpler arrangement than in the three Polydesmoids and, when seen in surface view, its anterior margin at the level of the intermediate cells appears perfectly even. The apparent pores which are most abundant over the pyloric eminences gradually become less numerous and disappear a short distance caudad of the pyloric valve. Where present, they are quite distinct, but appear as simple openings unassociated with any intracellular modifications below them. The rugae are always six in number, bluntly rounded and somewhat irregular in the anterior part of the gut but always becoming more and more sharply pointed and symmetrical toward the rectum. In the anterior region they may be reduced to slightly convex surfaces by expansion, while in the constricted posterior region, they are always well developed and may effect a complete closure of the lumen. Here they often present distinct angularities along their sides and at their ends, which give the lumen a very artistic outline suggesting that of a starfish. (See Figs. 50, 53 and 54.).

The intestinal intima of Scytonotus is so similar to that of Orthomorpha that one description will serve equally well for

both. Its anterior margin, in surface view, presents about twenty four symmetrical corrugations, which roughly correspond to the number of valvular infoldings, and, as I have already noted, it bounds the free margin of the latter as a simple layer. At a short distance caudad of this level, the intima becomes elevated over each cell individually in such a way that, when viewed in sagittal section, it appears distinctly serrate, with the apex of each component tooth projecting caudo-mediad, while in cross section it appears as a series of convexities each of which limits a single cell. At the apex of each convexity or tooth there is a caudo-medially directed, sharp pointed spine from 15 to 20 microns in length and with a basal part projecting well into the cytoplasm of the underlying cuboidal cell. The spine is continuous with the intima, but the latter is perceptibly thinner where it attaches to the former than elsewhere. Quite often in cross sections through this level, the spines appear double but united by a common base below the intima. In a number of my sagittal sections, I was able to trace delicate fibers extending caudo-lateral from the bases of the spines to the circular muscles and thus penetrating the cytoplasm and basement membrane of the epithelium. I also observed that some of the spines were pitched at a more perpendicular angle than the others and that in many instances their tips projected through the peritrophic membrane. In a previous section I mentioned the torn condition of the segments of peritrophic membrane covering the faeces in these two genera, and I am therefore justified in concluding that these spines are freely moveable, that they are elevated to a perpendicular position by

the contraction of the delicate fibers attached to their bases and that, in being so elevated, they tear or penetrate the peritrophic membrane. (See Fig. 55). As regards the ultimate object of this tearing or ripping of the latter, I can only suggest that it might either serve to bring digestible matter, which was not dialyzed through the peritrophic membrane, into contact with the enzymes, or simply aid in defecation. Spines somewhat analogous to those which I have just described, have been noted by Petrunkevitch (1900) and Sanford (1918) on the pads in the posterior region of the gizzard in Periplaneta but in this instance they are moved in the opposite direction by muscular contraction and thus help to force the food caudad into the midgut.

Caudad of the level to which I have just referred, the spines become less massive and increase their numbers to four or five for each cell. At the same time, their bases and the fibers attaching to them become less pronounced. From this point on to the level at which the Malpighian tubules open, the spines gradually increase in number and decrease in size until they appear as short and rather ill defined hair-like projections. Also the intima resolves itself into eighteen or twenty irregular flat rugae, while the epithelial cells become columnar and increase their height from 20, or less, to 30 microns. Throughout the greater part of the middle region of the intestine, the intima appears much the same as at the level of the Malpighian tubule openings, but in the constricted posterior region there is a semblance of six rugae which are decidedly more blunt and irregular than those at the corresponding levels in Parajulus. (See Figs. 55, 56 and 59).

In Fontaria the intestinal intima is simple throughout its entire course but reflected into very complicated, and greatly ramified folds wherever the gut is more or less contracted. But at levels along the dilated middle region of the intestine the latter are very much reduced and in some places entirely obliterated. (See Figs. 57 and 58). It is to be especially noted that Fontaria lacks all traces of spines which are so conspicuous in Polydesmus, Scytonotus and Orthomorpha and that, consequently, their presence cannot be looked upon as a character common to the group, Polydesmoidea. The intima of Fontaria resembles that of Scytonotus and Orthomorpha in presenting an uneven anterior margin, but the unevenness here takes the form of somewhat irregular pointed projections rather than rounded, symmetrical corrugations.

(c) Epithelium.

Except in Polyxenus, where Reinecke notes cuboidal and columnar cells irregularly alternating with each other at all levels, the intestinal epithelium is consistently referred to by the authorities as comprising typical columnar cells with more or less elyptical nuclei situated in their basal thirds and an even cytoplasm. They also observed a gradual decrease in the height of the cells caudad but mention no further deviations in shape or character.

The same general description holds for the intestinal cells of my own specimens, but the variations in height are more marked in Scytonotus and Orthomorpha than in Parajulus and are very extreme in Fontaria. Aside from the low intermediate layer already mentioned, the cells of Parajulus decrease in height from 40 to

30 microns in their posterior course (See Figs. 53 and 54), and, because of the rugae, there are no very appreciable changes due to the expansion of the lumen. In Scytonotus and Orthomorpha, as I have previously intimated, the spiniferous cells in the anterior region of the intestine increase posteriorly from a height of 18 or 20 to 30 microns at the level of the Malpighian tubule openings, and change from cuboidal elements with rounded nuclei to columnar with more or less elyptical nuclei. Posterior to this, the latter height and shape are quite consistently maintained all the way caudad to the rectum, but in these genera the relative deficiency of the rugae permits the height of the epithelium to become somewhat lessened under muscular expansion. (See Figs. 55, 56 and 59). The epithelium of Fontaria varies from a height of 60 to 10 microns in its posterior course, but is lower toward the caudal end of the dilated middle region than in the posterior region, being cuboidal in the former and columnar in the latter. It does not, however, show an even decrease at any level, and the cells at the apices of the folds are usually higher than those near the bases of the latter. (See Figs. 52, 57 and 58). In all four genera, the cytoplasm of the intestinal cells is finely but distinctly granular both ectad and entad of the elyptical nuclei, and delicate, parallel, spongeoplasmic fibers may be seen closely attached to the ectad surface of the intima. Quite commonly in Parajulus, large, clear vacuoles are present at the distal extremity of the cells. The basement membrane is thin and even but directly continuous with that of the midgut. In many cross sections through the intestine of Para-

julus the cut ends of densely massed tracheae are to be found at the bases of the rugae but well entad of the muscularis. (See Fig. 54.). Greatly coiled but analogously situated tracheae are prominent in longisectional views of the posterior region of the intestine in Fontaria.

(d) Muscularis.

In all of the Diplopods so far investigated the muscularis is described as more strongly developed over the intestine than in any other division of the tract and as consisting of inner circular and outer longitudinal layers. It is further noted that the fibers of both are of about the same diameter, but that the longitudinal are much fewer and more irregularly disposed than the circular, which are always close together and become densely massed about the constricted posterior region of the intestine, thus forming a sphincter. From Reinecke's figures, I would infer that this posterior sphincter is less marked in Polyxenus than in the other genera, but all the authorities represent the muscularis as ending abruptly at the point where the rectum begins. Effenberger refers to no sphincter over the cardiac valve or anterior and middle regions of the intestine of Polydesmus, but, with this exception, it may be said that the typical Diplopod intestine possesses an anterior sphincter over the pyloric valve or a short distance caudad of it and a posterior sphincter covering the entire posterior region and ending at the rectum. As I have already mentioned, Krug recognized, in addition to the other two, a middle sphincter in Julus Mediterraneus which he describes as

forming an incomplete ring about the anterior region of the intestine. It need hardly be said that both longitudinal and circular fibers are unanimously recognized as striated.

In the four genera under consideration, the fibers of both layers are of approximately equal size and have diameters which average between 6 and 9 microns in Parajulus, 4 and 7 in Scytonotus and Orthomorpha and 10 and 15 in Fontaria. Of these, the circular have an arrangement very much like that of the circular oesophageal muscles and are thus in close apposition throughout the length of the intestine and show obliquely interconnecting branches at irregular intervals. In Parajulus there is a fairly well defined anterior sphincter just caudad of the pyloric valve consisting of about three tiers of fibers, and an equally thick posterior one which is roughly confined to the whole posterior region. Scytonotus and Orthomorpha present a very prominent sphincter of five or six tiers of fibers immediately behind the openings of the Malpighian tubules which thus further marks off the anterior from the middle region of the intestine in these genera, and which, in the absence of a distinct corresponding structure from the pyloric region, might be here referred to as the anterior sphincter. Their posterior sphincter is very much like that of Parajulus but somewhat more concentrated toward the caudal extremity of the posterior region. In Fontaria, the circular fibers are disposed in a close series of very prominent sphincters beginning at the pyloric valve and ending about a millimeter posterior of the openings of the Malpighian tubules. Here thicknesses of ten or more tiers of fibers can be made out. Also

over the posterior region there are a series of thickenings rather than one more or less integral sphincter. (See Figs. 50 to 62).

The longitudinal fibers present an irregular distribution at all levels of the intestine and, as I have mentioned several times before, are formed by the fusion of groups of midintestinal longitudinals over the pyloric valve. Consequently they are always fewer than the latter, and, in proceeding caudad towards the rectum, become still fewer by this same process of fusion. Thus in Parajulus their number to the cross section decreases from approximately 70 to 55, in Scytonotus and Orthomorpha from 85 to 60 and in Fontaria from 140 to 100, or less. (See Figs. 50 to 62).

Attached along the sides of the posterior region of the intestine and extending caudo-laterad to their origin on the anterior margin of the anal segment are well developed groups of suspensory muscles that at once recall the dilators which are similarly situated in reference to the oesophagus. Other more widely separated fibers insert dorsally on the wall of the gut at the same level as the lateral ones and extend dorso-caudad to a similar origin, thus establishing a continuity between the right and left lateral groups. (See Figs. 60 and 61.)

Extending along the wall of the intestine of Parajulus for the greater part of its length and disposed in about six or eight more or less evenly spaced strands that are interrupted at various levels are groups of small, round cells with a clear vacuolated cytoplasm which is strongly suggestive of adipose tissue. In cross section they appear as small, compact clusters alternating with the longitudinal muscle fibers and having no definite re-

lationship with the underlying structures. (See Figs. 53 and 54). But in Scytonotus, caudad of the openings of the Malpighian tubules, similar cells are to be found in two series of much larger clusters situated on opposite sides of the gut. The latter become gradually smaller in their posterior course, and in cross section the smaller ones appear as solid masses of cells, while the large, anterior ones present a distinct central cavity which communicates by a narrow opening with the intestinal lumen and seems to be lined by a thin continuation of the intima. (See Fig. 59) Each series of clusters thus resembles a lobulated, caudally tapering gland lying close to the wall of the gut and opening into the latter at several points near the Malpighian tubule openings. In Orthomorpha and Fontaria I have observed similar series of clusters but no suggestion of central cavities or openings into the intestinal lumen. But whether these analogously situated structures in Parajulus, Orthomorpha and Fontaria are functionally related to those of Scytonotus or not, all of the positive evidence favors regarding the latter as intestinal glands.

(e) Summary.

1. In Parajulus, the Malpighian tubules open at the junction of mid and hindguts and the intestine is divisible into a long, wide anterior and a short, narrow posterior region. But in the Polydesmoids the former open at an appreciable distance posterior to the pyloric valve and thus subdivide the anterior region of the intestine into a short cephalic and a long caudal

portion.

2. In Parajulus a layer of low intermediate cells is prominent at the anterior extremity of the intestine while in the others the intestinal epithelium shows no marked differentiation at this point.

3. The pyloric valve of Parajulus comprises six symmetrical masses of cells which project well into the lumen and form the anterior ends of the six intestinal rugae. These may be referred to as the pyloric eminences. Their cells separate the intermediate layer from the remainder of the intestinal epithelium; but it is probable that the former constitute an integral though specialized part of the latter, and are neither genetically nor functionally related to connective tissue. In the Polydesmoids, these structures are supplanted by typical valvular inflections which are simple and regular in Scytonotus and Orthomorpha but complex and irregular in Fontaria.

4. The intestinal intima is a simple chitinous layer throughout its course, except in the vicinity of the pyloric valve in Parajulus where it is beset with numerous small pore-like structures, and the anterior region of the gut in Scytonotus and Orthomorpha where it presents muscularly moveable spines which tear and penetrate the peritrophic membrane.

5. The intestinal rugae of Parajulus are well developed, regular and six in number throughout their course. In Scytonotus and Orthomorpha they are poorly defined but more numerous anteriorly, while in Fontaria they are resolved into very prominent and complicated folds.

6. Caudad of the pyloric valve, the intestinal epithelium of Parajulus and Fontaria is columnar and homogeneous but gradually decreases in height posteriorly, the decrease being most pronounced in Fontaria. In Scytonotus and Orthomorpha, the anterior spiniferous cells are cuboidal but become columnar toward the opening of the Malpighian tubules and thence undergo very little or no reduction in height caudad.

7. In the intestinal muscularis of Parajulus, the circular fibers are disposed in an anterior sphincter over the pyloric valve and a much more extensive posterior one over the caudal region of the gut. The posterior sphincter in Scytonotus and Orthomorpha is much like that of Parajulus, but the anterior one, instead of being pyloric, is situated just caudad of the openings of the Malpighian tubules. In Fontaria there is a series of nearly contiguous anterior sphincters extending from the pyloric valve to a point a short distance behind the tubules' insertion and a similar series of posterior sphincters near the rectum.

8. In all four genera the intestinal longitudinals are irregularly distributed, fewer than the midintestinal with which they are continuous, and gradually decrease in number caudad by fusion with each other.

9. Intestinal dilator muscles suspend the posterior end of the hindgut to the anterior margin of the anal segment dorsally and laterally.

10. Caudad of the insertions of the urinary tubules in Scytonotus are masses of round, clear cells extending along the wall of the intestine and receiving diverticula from its lumen in a few places. It is probable that these structures are in-

testinal glands. More or less analogous structures are present in the other genera, but show no traces of cavities or ducts communicating with the intestinal lumen.

B. Rectum.

In every genus of Diplopod in which it has been studied, the rectum has essentially the same shape, and its dimensions correspond quite closely to those of the pharynx. It always presents two more or less distinct dilatations, of which the first is most prominent ventrally and laterally and situated immediately caudad of the constricted intestinal opening. The second, which occupies the midregion of the rectum, is more evenly developed on all sides but usually not so extensive laterad or ventrad as the first. Posterior to the dilatations, the rectum is either wide or narrow depending on whether the lateral anal valves are open or shut. When the latter condition obtains, the same may be entirely closed, and then appears externally as a long, median slit extending ventro-cephalad from the more or less overlapping dorsal scute and ending at the apex of a triangular sclerite known as the anal scale. Thus, because of the oblique position of the anus, the dorsal side of the rectum is longer than the ventral and, because of the adduction and abduction of the anal valves, the width of its posterior half is inconstant. On the other hand, its dorso-ventral diameter is quite constant posteriorly, while anteriorly both diameters are subject to the contraction and expansion of suspensory muscles.

All the authorities agree that the rectal intima is simple and similar to that of the intestine, but Effenberger (1909) de-

scribes it as gathered into many irregular folds in Polydesmus, while the others claims that it is smooth. On the epithelium observations vary widely. Reinecke (1910) figures it in Polyxenus as very much like that of the intestine but with the cells more uniformly cuboidal. Krug (1907) and Effenberger (1909) refer to it as distinctly lower than the intestinal in Julus and Polydesmus and showing no cell boundaries. Wernitzsch claims that the rectal epithelium is entirely lacking in Craspedosoma and figures the intestinal in sagittal section as abruptly dwindling to a point just cephalad of the rectum. As I have previously intimated, a rectal muscularis is universally regarded as lacking, while the intestinal is always shown as ending posteriorly with the intestine itself. Krug, Effenberger and Reinecke mention rectal suspensory muscles but refer to them in such a general way that I am unable to treat them comparatively. Wernitzsch maintains that the Craspedosoma rectum is entirely dissociated from muscle attachments of any sort, although he refers to the possibility of its being extruded and serving as a clasping organ in copulation.

(a) Intima.

In Parajulus and the three Polydesmoids under consideration, the general shape of the rectum, position of the dilatations and nature of the chitinous intima are essentially as described for the other genera. As might be inferred from its greatly reflected condition in the intestine, the rectal part of the intima in Fontaria is more folded and irregular than in the other three. Like the pharyngeal intima it is continuous with the primary chitin of

the exoskeleton, but at the point of transition with the latter it often appears thinner and slightly flexed on itself in such a way as to suggest a hinge. (See Fig. 62). When Mallory's stain is used, the outer part of the primary chitinous layer over the entire surface of the body is differentiated red and thus stands out in marked contrast with the blue of all the underlying chitin, but this red outer layer extends from the anus only a short distance cephalad along the free margin of the rectal intima. (See Figs. 60 to 65).

(b) Epithelium.

Contrary to the interprelations of Krug, Effenberger and Wernitzsch previously mentioned, Parajulus, Scytonotus and Orthomorpha present a rectal epithelium in which the cells are clearly distinguishable and very similar to those of the intestine. In the anterior part of the rectum they are relatively low, usually columnar but often cuboidal for short stretches and with a height averaging about 28 microns in Parajulus and 25 in Scytonotus and Orthomorpha. Toward the anus, however, a distinct, sometimes rather abrupt, increase in height is commonly noticeable, but this never exceeds the maximum height of the intestinal epithelium. The transition from rectal to hypodermal epithelium is very abrupt in these genera, and some of my Orthomorpha preparations showed very distinct bud-like clusters of small cells at this point, which are evidently rectal regenerative centers analogous to the rectal imaginal plates observed by Kowalevsky (1887) and others in insect larva. (See Figs. 62 to 64). In Fontaria the rectal epithelium is very low and cuboidal throughout. Here and there

the cells are even flat and less than 10 microns in height. The point of transition with the hypodermis is apparently not so abrupt in this genus as in the others, although this was not very clearly brought out in my sections. (See Fig. 64). In all four genera, the basement membrane is clearly definable, much like that of the intestinal epithelium and directly continuous with that of the hypodermis. (See Figs. 62 to 65).

(c) Suspensory Muscles.

In all four genera, there are two groups of suspensory muscles which insert on the apices of the somewhat anteriorly inclined first and second dilatations respectively. The fibers of both groups are quite evenly distributed throughout the circumference of the rectum and pass obliquely forward to originate, in common with the intestinal dilators, on the anterior margin of the anal segment. In correlating the changes in the shape of the rectum during defecation, which I have been able to carefully observe in a number of semi-transparent, immature Parajuli and Orthomorpha, with the position of these muscle attachments, I have been able to determine the particular role that each group plays in this process. After faecal matter has entered the rectal lumen, the intestinal dilators, by contraction, force the constricted end of the intestine toward the anus, thus decreasing the length of the rectum and pushing the faecal matter caudad. At the same time, the rectal dilators contribute to this result and also widen the rectal lumen by pulling the dilatations toward the anterior margin of the anal segment. As the end of the intestine is brought nearer and nearer the anus, it obviously forces the

anal valves apart and thus effects the expulsion of the faecal matter. (See Figs. 60 and 61).

D. Summary.

1. In all four genera the rectal intima is simple and directly continuous with the primary chitin of the exoskeleton.

2. The rectal epithelium of Parajulus, Scytonotus and Orthomorpha is quite similar to that of the intestine and its transition with the hypodermis is abrupt. But in Fontaria it is very low, cuboidal or flat, never columnar and its transition with the hypodermis is probably gradual.

3. The rectum has no muscularis, but is suspended from the body wall on all sides by two groups of rectal dilators which insert on the apices of the first and second dilatations respectively and have an origin in common with the hind-intestinal dilators on the anterior margin of the anal segment.

V. ASSOCIATED GLANDULAR STRUCTURES.

Under the above heading, I shall record my observations on a number of structures which, only from a loose morphological standpoint, may be considered as forming part of the digestive system. These are, in serial order proceeding caudad, the anterior and posterior salivary glands, tubular glands, Malpighian tubules and anal glands.

I. Anterior Salivary Glands.

Lying quite close to the dorsal wall of the pharynx just cephalad of the brain, is a more or less compact mass of tissue

which has been found present in all the Diplopods examined in this connection and which appears white in fresh dissection and sufficiently lobulated to be easily mistaken for a fat body. It was first recognized as such in Julus by Visart (1895) who regarded it as a cephalic continuation of the perintestinal fat bodies which lie laterad of the digestive tract in the trunk. For the same genus Rossi (1902) still considered it fat but claimed that it was entirely dissociated from the perintestinal fat bodies. Then Silvestri (1902), upon carefully dissecting this tissue in Pachyiulus communis, found that it constituted an anterior and a posterior pair of very closely united glands which open into the pharynx by corresponding pairs of slender, thin-walled ducts. Of these, he describes both as inserting dorso-laterad, but the anterior at a level midway between mouth and oesophagus and the posterior near the caudal extremity of the pharynx. Since the two openings of the former are over three times as far apart as those of the latter, he refers to the anterior pair of glands as the 'glandulae buccales laterales' and to the posterior as the 'glandulae buccales mediales'. He figures both pairs of ducts as central axes giving off ramifying collateral branches at fairly regular intervals and shows the posterior or medial pair as somewhat larger than the anterior or lateral, but presents no drawings of the glands themselves and has nothing to say regarding their histological structure. A short distance cephalo-mediad of each lateral opening, Silvestri figures an oval body which he labels 'palatine gland', but does not describe. This is the only reference to such structures which I have been able to find in Diplopod literature and I have not discovered anything that might cor-

respond to them in the genera which I have studied. I can therefore only suggest that they may represent specialized, thickened portions of the pharyngeal epithelium which are either lacking or inconspicuous in many Diplopods. Krug (1907), Effenberger (1909), Wernitzsch (1910) and Reinecke (1910), however, all recognize the buccal glands and adopt Silvestri's interpretations, but describe them as a single pair opening dorsally on the pharynx by a single pair of ducts and thus hold themselves open to the suspicion that they entirely overlooked one or the other pair. From their rather general descriptions and diagrammatic figures, it is probable that the ducts which they observed are the anterior or lateral ones of Silvestri, though Effenberger and Reinecke admit not having definitely located their openings. For Julus, Craspedosoma and Polydesmus, the glands are described as botryoidal in their outward appearance and as comprising a thick mass of rounded cells closely investing a central duct, but no mention is made of nuclear structure or the interrelationship between the cells and the duct. Reinecke refers to the glands in Polyxenus as situated on each side of the head near the base of the antennae, and thus implies that the right and left elements are more distinctly separated than in the other genera. He also figures the glands in cross section as consisting of a relatively large chitinous duct enveloped by an epithelium of low, small cells and outside of this, by a high columnar layer with ectally situated nuclei. Assuming that his representations are correct, it may be reasonably claimed that these glands more closely approach their archetype in Polyxenus than in the other genera, since the

paired ducts argue an originally paired condition for the glands and a simple epithelium is generally recognized as more primitive than other epitheloid dispositions of fixed cells. In my further reference to these glands, I shall use the term 'anterior salivary' proposed by Krug and adopted by his successors, not because it is more descriptive, but more convenient than Silvestri's 'glandulae buccales laterales et mediales'.

In Parajulus, Scytonotus and Orthomorpha, the anterior salivary glands are essentially similar in size, position and shape, though a little smaller in proportion to the dimensions of the head in Parajulus. When their entire extent is shown in sagittal section they are seen to overlie the posterior three fifths of the dorsal pharyngeal wall and to have a maximum thickness of about one fourth of their length. In cross section their appearance seems to vary somewhat in different individuals, but posteriorly it usually takes the form of an integral mass nearly as wide as the protocerebrum in Parajulus and even wider in Orthomorpha. Anterior to this level, the tissue is often resolved into three distinct but closely united lobes in Parajulus, one medial and two lateral, while Orthomorpha shows a very symmetrical division into two. At serial levels cephalad from this point, the glands in both genera appear successively thinner and are disposed into two, rarely four, closely apposed lobes. The anterior extremity, when viewed in cross section, takes the form of a shallow strip of dense tissue showing no suggestion of lobes. It will thus be seen that in Parajulus and Orthomorpha the glands are quite consistently united throughout their length but more closely fused anteriorly and posteriorly than elsewhere. The

lobular disposition of the tissue is definitely correlated with the main branches of the ducts which in cross section are seen to occupy the center of each lobe and are broken up into numerous small branches at the non-lobate anterior and posterior extremities. As I have previously mentioned, the second and third groups of dorsal dilator muscles interrupt the glandular tissue in their transit dorsad from the superior wall of the pharynx. In cross sections at or near the levels where they attach to the latter, the glands appear divided into four or more separate and subequal parts, but these are not to be confused with the true lobes. In Scytonotus my material was too limited to enable me to study the glands in cross section, but in longisection they appear topographically similar to those of Orthomorpha. The glands of Fontaria, which, aside from fresh examinations, I have seen only in longisection, are similar in general shape and extent to those of the other genera but much more irregular and diverticulate. (See Figs. 1, 2, 3, 4, 6 and 7.).

A. Ducts.

In Parajulus and Orthomorpha I have obtained quite satisfactory sectional views of the ducts of the anterior salivary glands at the levels where they open into the pharynx and find that both the anterior and posterior pairs are present. I have also identified the openings of the posterior pair in fresh dissections of Fontaria and have seen the ducts sufficiently well in longisections of the head of Fontaria and Scytonotus to be reasonably sure that they are essentially similar in all four genera. Both pairs in Parajulus and Orthomorpha open at the same

points as those of Pachyiulus, according to Silvestri; the anterior dorso-laterad at the middle plane of the pharynx and the posterior dorso-laterad at the caudal extremity of the pharynx. (See Fig. 5). The posterior ducts, however, penetrate the pharyngeal epithelium and intima at such an oblique angle that their actual openings are well within the oesophageal lumen at a level directly below the brain. (See Fig. 61). Distad of their openings, the ducts proceed dorso-cephalad for a short distance and then divide into an anterior and a posterior branch, both of which run parallel to the dorsal wall of the pharynx, give off collateral branches along their course and gradually dwindle toward their free ends. The ducts enter the glandular tissue immediately after leaving the pharyngeal epithelium and the anterior pair seems to distribute over a more limited extent of tissue than the posterior, but, because of the apparent continuity of the ducts in serial cross section between the two pairs of openings, I believe that the main posterior branch of the former anastomoses with the main anterior branch of the latter. A more careful anatomical study than I have been able to make will be necessary, however, before this point can be verified. (See Figs. 65, 66 and 67).

Histologically both pairs of ducts are similar. Entad they are lined by a chitinous intima which is directly continuous with that of the pharynx and becomes so thin distally that it is hardly perceptible in the smaller branches of the ducts. The latter may be readily confused with tracheae which ramify abundantly throughout the glandular tissue and, especially in Orthomorpha, are often disposed in compact bundles closely apposed to one side

of the larger branches of the ducts and running parallel with them. There is nothing to indicate, however, that either the ducts or the tracheae terminate intracellularly in connection with the gland cells. Near their openings the former are invested by a closely defined, almost cuboidal epithelium, continuous with that of the pharynx and, in Parajulus, containing a fine yellowish brown granulation which is noticeable in fresh material. But, after traversing the glandular tissue for a short distance, this narrows down to a very flat layer and its nuclei, round and clear at first, become dark and fusiform. Though hardly distinguishable in the smaller branches of the ducts, it is safe to assume that the epithelium is present wherever the chitinous intima obtains. (See Figs. 65 to 71).

B. Gland Cells.

The tissue of the anterior salivary glands comprises large, irregularly rounded cells with relatively small, elliptical, sometimes angular nuclei, and in a fresh state, as well as in many of my Flemming-iron haematoxylin preparations, it is very suggestive of the perintestinal fat bodies. There are, however, a number of respects in which these cells together with the very similar cells of the posterior salivary glands, differ tinctorially from the latter. 1. They do not begin to show any discoloration until after four minutes subjection to osmic acid while the fat bodies blacken immediately. 2. After being stained three minutes in Sudan III and then washed in distilled water they show only a light pinkish tinge but the fat bodies appear bright scarlet. 3. Under Bouin's fixation, their cytoplasm stains quite

deeply and uniformly with haemalum and other reagents, while the fat cells are always lightly stained. Moreover, the cells of the anterior glands differ from those of the posterior in taking a blue or bluish purple rather than a deep reddish purple stain under Mallory.

In Scytonotus my gland material was so poorly fixed that it yielded no satisfactory results, but in the remaining genera the cells were very clearly brought out and, in all, two types are plainly distinguishable. The cells of one type are usually smaller than those of the other, the nuclei proportionally larger and centrally situated and the cytoplasm uniformly darker and distinctly granular. In the second type, the cytoplasm is clear and vacuolated and the nuclei are often eccentric, somewhat shrunken and darkly stained. At certain levels in transverse sections only one or the other type may be recognized, but more often both can be seen together, either in more or less well defined groups of similar cells or irregularly interspersed. Also intermediate cells, with the peripheral part of the cytoplasm vacuolated and the part near the nucleus granular are of common occurrence. The foregoing observations would indicate that the two types represent different stages in the elaboration of secretion, and that the larger, vacuolated cells show a more advanced stage than the others. Some of the granular cells appear noticeably smaller than others, but I have observed nothing indicative of regenerative centers. I am therefore inclined to belive that, like the typical serous cells of Vertebrates, which they suggest, these elements may repeat the secretory cycle an indefinite number of times before undergoing final degeneration and

replacement. (See Figs. 68, 69 and 70). In some of my Orthomorpha sections, a peculiar intracellular structure consisting of rather dense, radially arranged spongioplasmic filaments was frequently found near the nuclei of the larger cells. (See Fig. 69.).

C. Summary.

1. In all four genera, the anterior salivary glands are situated dorsad of the pharynx and anterior to the brain, but their tissue is more lobate and branched in Fontaria than in the other genera.

2. In Parajulus and Orthomorpha, the glands open into the pharynx by two pairs of ducts; an anterior pair which inserts dorso-laterally at a level midway between mouth and oesophagus and a posterior which inserts dorso-laterally at the caudal extremity of the pharynx.

3. Both pairs of ducts divide into main anterior and posterior branches shortly after entering the glandular tissue and from these, in turn, smaller collateral branches are given off, but there are no indications of intracellular endings.

4. The ducts are lined throughout by a chitinous intima which is very thin in the smaller branches but continuous with the intima of the pharynx.

5. The ducts are likewise invested throughout by an epithelium continuous with that of the pharynx, almost cuboidal near the openings of the latter, but very flat within the glandular tissue. In Parajulus the epithelium presents a fine yellowish brown granulation in its thicker proximal portion when examined

fresh.

6. The gland cells react differently toward osmic acid and Sudan III, than the perintestinal fat cells. They differ from the posterior salivary gland cells in staining bluish purple rather than reddish purple under Mallory.

7. In the early stages of their secretory cycle, the gland cells are relatively small with centrally situated nuclei and dense granular cytoplasm, while in the later stages the nuclei are more or less eccentric and the cytoplasm clear and vacuolated.

2. Posterior Salivary Glands.

The posterior salivary glands, to use Krug's (1907) term, comprise a pair of whitish masses of tissue lying along the dorso-lateral sides of the oesophagus throughout its entire extent in the trunk (except in Polyxenus where the latter is confined to the head) and gradually increasing in thickness and width caudad until they form a more or less continuous ring about the cardiac valve. Like the anterior salivary glands, they too were looked upon as perintestinal fat bodies by the earlier investigators, Plateau (1878), Visart (1895) and Rossi (1902), while the distinction of demonstrating that they are glands falls to Silvestri (1902) who found their ducts and described them as opening into the pharynx ventro-laterad and just below the premandibles in Pachyiulus. He refers to the glands as 'glandulae mandibulares' and regards them as homologues of the mandibular glands of insects, which have been recognized in Collembola by Willem (1897), in larval Lepidoptera and Trichoptera by Henseval (1897,A. and B.)

in Mantis religiosa and adult Hymenoptera by Bordas (1894,1906) and are very comprehensively treated by Berlese (1910, page 507). Silvestri, however, neither figures the glands nor mentions their histological structure. Krug (1907), Effenberger and Wernitzsch (1910) describe them as very similar to the anterior salivary glands and as consisting of large, round cells with small nuclei enveloping central ducts. Reinecke (1910) also represents them as comprising large round cells and thus finds them quite different from the anterior glands in Polyxenus. All the authorities are agreed that the ducts insert ventro-laterally on the pharynx, though Effenberger and Reinecke were unable to see the openings. Krug refers to the glands of Julus as fused posteriorly and completely enveloping the oesophagus, while he figures the walls of the duct in longisection as a low columnar epithelium with slightly granular cytoplasm and round, ectally situated nuclei. Wernitzsch shows them investing the base of the oesophagus dorsally and laterally in Craspedosoma but never entirely surrounding it as a ring, while Effenberger claims that they are paired throughout in Polydesmus and confined to the dorsal oesophageal wall. By Reinecke they are diagrammatically represented as forming a continuous ring about the middle third of the oesophagus and entirely absent from the posterior third in Polyxenus. In sections through the anterior region of the trunk, Bruntz (1904) figures the glands of Glomeris as lying dorsad of the oesophagus, but labels them connective tissue and does not mention them in any part of his text. As I shall point out more clearly in connection with the tubular glands, this failure to identify the real posterior salivary glands of both Julus and Glomeris has been the

chief obstacle holding back his labial kidney hypothesis from general recognition.

In Parajulus the posterior salivary glands have much the same distribution and external structure as those of Julus, but show a greater development in some individuals than in others. Thus at the posterior extremity of the oesophagus, while they often appear in cross section as a thick, continuous ring, they are still more commonly divided into lobes of variable size and number and do not invest the former ventrally. Anterior to this level, the glands are distinctly paired and each element more or less widely separated into a dorso-lateral and a lateral lobe. (See Fig. 16); while still farther cephalad the lobes gradually resolve themselves into a single pair of dorso-lateral masses which decrease in size toward the head and thence continue as simple epithelial ducts to their openings. (See Fig. 14). The glands of Scytonotus, Orthomorpha and Fontaria are like those of Polydesmus and are always less extensive laterad or ventro-laterad than in Parajulus, but more so in Scytonotus and Orthomorpha than in Fontaria. They invest the oesophagus dorsally and laterally at its posterior extremity and each is divided into three or four lobes, but throughout the remainder of their course are undivided and dorso-lateral. In comparing the glands of the four genera, it will be seen that their thickness and width is almost inversely proportional to the extent to which the tubular glands are coiled along the ventro-lateral sides of the oesophagus, which is greatest in Fontaria and least in Parajulus. See Figs. 1, 2, 3, 4 and 71.). Though I have observed them in sagit-

tal section only in Parajulus and Orthomorpha, the pharyngeal openings of the ducts are the same in all and when seen in surface view appear just behind the bases of the internal maxillary laminae and nearer the medial than the lateral margins of the external stipites. (See Figs. 71 and 72).

A. Ducts.

From their openings the ducts extend dorso-caudad and laterad of the proximal parts of the tubular glands, which they cross obliquely in ascending to their dorso-laterad positions along the oesophagus. In their ascent they pass through the lateral parts of the central tendon and, just below this level, each receives the insertion dorso-medially of a pair of muscle fibers originating on the latter and dorso-laterally the attachment of a slender tendon which runs directly forward to the medial basal angle of the premandible. (See Fig. 73). The muscles and tendon are evidently instrumental in controlling the discharge of the secretion and the tendon is so suggestive of a slender chitinous duct that I interpreted it as such in my earlier dissections. In Parajulus the glandular tissue commences at a somewhat variable distance caudad of the level where the ducts assume their dorso-lateral position along the oesophagus which is just anterior to the pseudocciput. But in the Polydesmoid genera it begins farther cephalad in the head and below the point at which the oesophagus is reached. Within the glands each main duct occupies a central position and branches posteriorly in accordance with the number of lobes into which the tissue is divided, each main branch

occupying the center of each lobe. As in the anterior salivary ducts, numerous collateral branches are given off throughout the extent of the glands. (See Figs. 13, 14, 16, 17 and 18). Between their pharyngeal openings and the glands, the ducts present an even caliber which is usually about half that of the tubular glands near their exits and therefore 25 microns in Parajulus, 22 in Scytonotus and Orthomorpha and 40 in Fontaria. In Parajulus, however, their lumens are sometimes so dilated that their diameter equals that of the latter. Histologically, the ducts are very similar to the anterior salivary. They are lined by a chitinous intima, continuous with that of the pharynx, much reduced within the glandular tissue and without intracellular endings, while their epithelia are low cuboidal, show a prominent yellowish brown granulation in Parajulus when examined fresh and are flat and inconspicuous throughout their distribution in the glands. (See Figs. 72 to 77.). As I have already intimated, the ducts often contain a secretion which stains a uniform dark blue under Mallory. (See Fig. 75).

B. Glands Cells.

Structurally, the cells of the posterior salivary glands are alike in all four genera and so suggestive of those of the anterior in every respect, that practically nothing remains to be said about them. It must be noted, however, that the distinction between the earlier and later secretory stages is often more sharply brought out in the former than in the latter, and that I was unable to observe anything analogous to the radial spongioplasmic bodies of the anterior gland cells in Orthomorpha. I

have already mentioned that both glands react similarly toward osmic acid and Sudan III, but that the posterior stain reddish purple rather than bluish purple under Mallory. (See Figs. 74 to 77).

C. Summary.

1. The posterior salivary glands invest the oesophagus dorso-laterally throughout its entire length in the trunk. The glandular tissue begins in the posterior region of the head but further forward in the Polydesmoid genera than in Parajulus.

2. In all four genera the glandular tissue increases in thickness and width posteriorly, but, while in Parajulus the two glands may fuse together and surround the base of the oesophagus as a ring, they remain paired throughout in the Polydesmoids and never cover more than the dorsal and lateral sides of the latter.

3. The glands are proportionally most developed in Parajulus where the tubular are smallest, and least developed in Fontaria where the tubular are largest.

4. In all four genera, the ducts of the posterior salivary glands open ventro-laterally into the pharynx. Their orifices are simple and situated just behind the bases of the internal maxillary laminae.

5. The ducts penetrate the lateral extensions of the central tendon in their course dorso-caudad to the oesophagus, and are attached to the central tendon by muscle fibers and to the premandibles by a pair of very slender tendons.

6. Both ducts and gland cells are very similar histologically to those of the anteriorly salivary glands, and the intima

and epithelium of the former are directly continuous with those of the pharynx.

3. Tubular Glands.

Though mentioned by a number of earlier authors, the tubular glands were first clearly described by Plateau (1878) who calls them, 'anterior salivary glands' in Julus and Glomeris. In the former he refers to them as a pair of long, slender, tube-like glands which open into the buccal cavity by a straight neck and thence proceed caudad along the sides of the digestive tract to a point a little in advance of the pyloric valve. Here they bend sharply on themvelves, become reduced by about two thirds in diameter and, following a greatly coiled course along the sides of their straighter proximal parts, ascend toward the head where the they end blindly a short distance anterior to the pseudocciput. Plateau notes the same essential plan of structure in Glomeris but finds that the descending proximal and ascending distal parts are both of the same diameter, greatly coiled throughout their distribution in the trunk and distinctly separated from each other. He also records that their tissue in both genera always shows a neutral or weakly alkaline reaction toward blue litmus paper and was therefore inclined to regard them as salivary gland, since in his earlier tests of insect salivary glands (1874) he obtained similar reactions. Rossi (1902) in Julus communis found that the glands do not open into the buccal cavity as Plateau had supposed, but at the bases of the interstipital grooves which form the dividing lines between the external and internal stipites on the ventral side of the gnathochilarium, and run straight forward as almost enclosed

chitinous canals to open at the distal extremity of the latter. Because of the complete dissociation of their openings from the pharynx, Rossi doubts the salivary function of the glands and refers to them simply as 'anterior glands'. In other respects his description corresponds very closely to that of Plateau for Julus except that he finds the ascending and descending rami not merely contiguous but invested by a common hyalin membrane. Silvestri (1902) refers to them in Pachyiulus as the 'glandulae maxillares' and thus recognizes them as homologous with the maxillary glands of insects which have been identified in Collembola by Willem (1897), in larval Trichoptera by Henesval (1897, A. B.), in adult Ichneumonids by Bordas 1894) and are described in resume by Berlese (1910, page 507). Beyond confirming Rossi's observations as regards the openings of the glands and expressing his own belief that they are salivary, Silvestri has nothing further to say, but it is obvious that he bases his interpretation of their relationship to insect glands upon the generally accepted homology between the Diplopod gnathochilarium and the Hexapod maxillae. Krug's (1907) observations on Julus Mediterraneus are in perfect accord with those of Plateau, Rossi and Silvestri on Julus and Pachyiulus, but, while regarding the glands as salivary, he proposes the term, 'tubular' in order to distinguish them from the anterior and posterior salivary glands. For much the same reason, and because it implies no definite function, I have adopted this term in referring to these structures. Krug also figures the epithelium of both ascending and descending rami as composing low columnar cells with a slightly granular cytoplasm and small, centrally placed ovoid or round nuclei. Effenberger (1909) finds that in Polydesmus

the openings of the tubular glands are similar to those of Julus but describes each descending ramus as dividing into a number of short, retrorse, digitiform branches at its posterior extremity which is laterad of the cardiac valve. This condition is so fundamentally at variance with all the other interpretations, not only of remotely related genera but also of the three Polydesmoids to be considered presently, that I am inclined to credit it to inaccurate observation. Effenberger represents the epithelium as high columnar with small dark nuclei situated very near the ental margin of the cells. He also observed that, during the act of feeding, a secretion from the opening of the glands is liberated over the food before the latter is taken into the pharynx. Reinecke (1910) notes the glands of Polyxenus as opening by a single median cleft between two sensory cushions which, in the Pselaphognaths, probably correspond to the lobi linguales in the very different gnathochilarium of the Chilognaths. He furtherdescribes them as entirely confined to the head, of even diameter throughout, and with a very short ascending part which presents a caudally directed, blind free ending. Heathecote (1890) in the same species, P. lagurus, and Issajew (1911) in P. lucidus refer to the tubular glands as extending an appreciable distance caudad in the trunk. Their epithelium is figured by Reinecke as cuboidal with large somewhat irregularly disposed nuclei, a slightly vacuolated or granular cytoplasm and indefinable cell boundaries. Wernitzsch (1910) describes the openings of Craspedosoma as similar to those of Julus, but finds that the glands extend caudad only as far as the cardiac valve and that the ascending and descending parts are of subequal caliber and distinctly separate throughout their course. He refers to the epithelium as

high columnar with round or ovoid nuclei nearer the ental than the ectal margin of the cells, but claims that the latter are relatively wider and lower in the right gland than in the left. Furthermore, he notes that the ascending parts end a short distance cephalad of the pseudocciput in a pair of large, ventrally contiguous sacks, situated ventro-laterad of the oesophagus and invested by a layer of widely separated, high cells broadly attached to a basement membrane but distally rounded. These elements appear very much larger than the epithelium of the remaining parts of the gland and contain small central nuclei as well as prominent granules at their free ends. Wernitzsch compares these sacks with mesodermal nephridial funnels and suggests that they may have originated as such but were later constricted off from the coelome by the closure of their internal openings. He also recognizes the similarity between the remainder of the glands and the tubular ectodermal parts of the nephridia, and concludes that the entire structures are homologous with the salivary glands of Peripatus which, according to Sedgwick (1888) and others, develop as modifications of a pair of embryonic nephridia belonging to the third cephalic segment and having an excretory function in the earlier instars of Craspedosoma, adheres to the prevailing view that they are secretory in the adults and suggests that their secretions may function as a cleansing fluid for freeing the mouth parts from particles of dirt which tend to encumber them.

In a comprehensive paper treating of the results of the injection of ammonium and indigo carmine into the body cavities of a large number of Arthropods, Bruntz (1904) includes some very illuminating observations on the behavior of the tubular glands of

Julus and Glomeris toward these reagents. In the first place, he finds that the ascending parts of the glands do not end blindly as Plateau, Krug and others maintain, but open into thin-walled, sack-like structures corresponding in position to the sacks just referred to in connection with Craspedosoma but histologically different. Bruntz does not figure these structures in Julus but refers to them as situated laterally in the posterior part of the head and as uniting with each other ventrad of the oesophagus. For Glomeris he figures them as ventro-lateral to the oesophagus in the anterior part of the trunk and describes them for both genera as very irregular in shape and as comprising a large central chamber, into which the ascending part of the gland opens posteriorly, and a great number of unequal secondary chambers peripheral to the central one and communicating with it. He also mentions the epithelium forming the wall of the structures and the partitions between the chambers as composed of small cells. In the second place, Bruntz finds that, following the injection of ammonium and indigo carmine into the body cavity, the former is taken up by the sack-like structures and the latter by the remainder of the tubular glands. He further observed that this behavior was constant in all his experiments but that the indigo carmine was absorbed much more rapidly by the tubular part of the glands (ten minutes after injection) than the ammonium carmine by the sack-like structures (from fourteen hours to two days after injection). But, because both reagents were taken up and eliminated, Bruntz regards the entire structures as 'labial kidneys' and refers to the sack-like bodies as the 'sacculi' and the tubular parts as the 'labyrinths'. In a critique of Krug's observations on Julus

Mediterraneus, Bruntz (1908) considers that Krug, in describing the posterior salivary glands, is referring unknowingly to the sacculi of the tubular glands. (The term, labial kidney, might be objected to on the ground that the structure on which they open is homologous with the maxillae rather than the labium of insects.). He is therefore surprised at Krug's mention of the posterior salivary ducts and recognizes the lateral chitinous extensions of the central tendons, which I referred to in connection with the tentorium, as the structures which he thinks Krug has mistaken for ducts. From this it can be readily surmised why subsequent investigators, who observed the more conspicuous posterior salivary glands but failed to find the sacculi, accepted Krug's and rejected Bruntz's interpretation of the tubular glands.

Though I have not tested out the function of the tubular glands with vital stains in Parajulus and the three Polydesmoids, their structure in these genera agrees so closely with Bruntz's descriptions that I am strongly inclined to regard them as excretory and can see no objection to designating their parts as labyrinth and sacculus.

A. Labyrinth.

As in other Diplopods, the labyrinths in all four genera open into the bases of the interstipital grooves which are more completely enclosed in the Polydesmoids than in Parajulus. In the latter, the diameter of the tube is subequal throughout and averages about 45 microns, except for a short distance caudad of its opening where it narrows down to about half of this dimension. Its backward course is nearly parallel with that of the posterior salivary duct until it reaches its ascending part or ramus in

the posterior region of the head, ventro-lateral to the oesophagus. From this point on, both rami are very closely apposed and may be easily mistaken for a single duct, greatly coiled along the ventro-lateral sides of the oesophagus but becoming less coiled toward its posterior extremity which is at the caudal end of the anterior third of the midgut. (See Figs. 1 and 71 A.). The labyrinths of Scytonotus and Orthomorpha are very much alike, have an average diameter of 40 microns and a cephalic distribution which is very similar to that of Parajulus. Caudad from the head the descending ramus pursues a coiled course along the sides of the oesophagus to the cardiac valve where the coils are very pronounced and intricate, but the ascending ramus runs forward to the sacculus as an almost straight tube lateral to the posterior salivary glands and entirely separate from the descending ramus. (See Figs. 2, 3, and 71 B. and C.). In Fontaria, the labyrinth which has an average diameter of 100 microns, differs from those of the other Polydesmoids only in being relatively more coiled toward its posterior extremity and in presenting an ascending ramus which is almost as coiled as the descending. (See Figs. 4 and 71 D.). It will be seen that the labyrinths in these Polydesmoids are very different from Effenberger's interpretation regarding Polydesmus.

Histologically the labyrinths present no distinctive differences in the genera under discussion. The narrow part of the tube just caudad of its opening shows a thin chitinous intima which is continuous with the primary chitin of the interstipital groove and ends abruptly at the point where the diameter begins to increase. Ectad of the intima the epithelium is cuboidal with round central nuclei, is proximally continuous with the gnathochilarial hypoder-

mis and distally resolves itself into a columnar layer with a greatly increased thickness and more or less elliptical nuclei. (See Fig. 83). From this point on, the cells of the labyrinth are essentially alike but relatively narrower and taller in Fontaria than in the others, and their average height is 12 microns in Parajulus, 10 in Scytonotus and Orthomorpha and 18 or 20 in Fontaria. They are broadly attached to a thick non-cellular basement membrane which is brought out very clearly in Mallory's stain, and ectad of which connective tissue cells may be seen closely investing the tube at various levels. Usually a cuticular border with a prominent basilar membrane but rather poorly defined processes is present and at such times the entire cytoplasm of the underlying cells appears homogeneous or slightly granular. (See Fig. 77, A, B. C and D, and Fig, 82 A.). At other times, the cuticular border is wholly lacking while the distal half or third of the cells is charged with large clear vacuoles and bulges well into the lumen. (See Fig. 82 B.). This undoubtedly represents a stage in the functioning of the cells in which the secretion or excretion is being released in a fluid state. Apparently the cuticular border may be cast off from a considerable extent of the eipthelium at one time (See Fig.77 D.), and it would seem that this is primarily due to the pressure exerted by the accumulating discharge products beneath it. While I have examined serial sections which would indicate that all the cells of the labyrinth may be in the cuticular border stage simultaneously, the cells in active discharge are always confined to limited areas, and in some of my longitudinal sections, the elements on one side of the tube are in one stage and those on the opposite side in the

other. Here and there, basal striations are faintly discernible, but ectad of the nuclei the cytoplasm always presents much the same appearance regardless of the conditions manifested by the distal parts of the cells. (See Fig. 77 A.). At various levels the epithelium is invaded by numerous tracheae which is some instances can be traced to the points where they pass through the basement membrane. They are usually inserted between the basal parts of the cells and appear to end blindly a short distance ectad of the lumen while the dark, fusiform nuclei of their end cells contrast markedly with the clearer, ovoid nuclei of the columnar elements. (See Fig. 82.A.). The lumen ordinarily shows no evidence of solid content, tnough occasionally a fine granular coagulum is present. In cross sections through the labyrinth of Parajulus at all levels in the trunk, the ascending and descending rami are seen to be invested by a common basement membrane and their adjacent epithelia sometimes appear confluent but usually a thin strand of small connective tissue cells is discernible between them. (See Fig. 77,A.). I have found no indications of muscle fibers ectad or entad of the basement membrane in any of my specimens.

I have already referred to Effenberger as having observed a secretion given off from the openings of the interstipital Grooves by Polydesmus while feeding. In Parajulus and Orthomorpha, I have noted the same phenomenon many times and under such favorable circumstances that I am certain the secretion came from the openings in question and not from the pharynx. Before the mouth parts are brought into play, the food is tapped several consecutive times by the head and, during this procedure, droplets of a

clear fluid exude from the distal end or ventral side of the gnathochilarium. Every time the latter touches the food one or more droplets are freed from it and form a surface film which is later taken into the pharynx together with the solid matter underlying it. This observation would indicate that a digestive ferment might be given off from the interstipital groove but, in view of the strong evidence pointing toward an excretory function for the tubular glands, it is irreconcilable with the latter interpretation, unless it can be demonstrated that some other glands take their exit in common with the tubular. In Orthomorpha I have found a pair of glands which might very well fill this requirement. They are situated ventro-laterally in the head a short distance caudad of the pharynx and each consists of a loose aggregation of alveoli with separate ducts which unite in opening into the base of the interstipital groove just anterior to the opening of the tubular gland. The ducts are quite slender and lined by a very thin chitinous intima which continues into the alveoli, but are invested by a flat epithelium which, unlike the cells of the anterior and posterior salivary ducts, appears to be in direct continuity with the alveolar gland cells as in the maxillary glands of Trichoptera larva. (See Henseval, 1897,A). In other respects, the cells of the aveoli are very similar to the anterior and posterior gland cells and show no trace of intracellular endings. (See Fig. 83.). I have observed similar glands in Parajulus but not so clearly as in Orthomorpha and in none of my sections have I been able to distinguish the opening of their ducts. As an appropriate name for these structures, I would sug-

gest the term, maxillary or gnathochilarial glands.

B. Sacculus.

In all four genera the sacculi are essentially alike and in close accord with the observations of Bruntz regarding their morphology. They are proportionally larger in Polydesmoids than in Parajulus but in all, are roughly pyramidal in shape with the broad bases of the pyramids cephalad and the apices where the labyrinths open, caudad. The walls and partitions are thin throughout but relatively thicker in the posterior region of the central chambers than elsewhere and the structures are prevented from collapsing by several important attachments. Cephalad they interconnect ventro-medially beneath the oesophagus and are dorso-medially attached to the dorsal side of the oesophagus by tendinous fibers which present small flat cells at irregular intervals along their courses. (See Fig. 78). By similar fibers they attach dorso-cephalad to the ends of a pair of slender apodemes extending ventro-caudad from the bases of the antennae. (See Fig. 80). Ventro-laterally they are quite broadly joined to the lateral, septate extensions of the chitinous central tendon (See Fig. 80) and cephalo-laterad to the posterior extremities of the mandibular apodemes in the Polydesmoids or the more medial posterior processes of the tentorium in Parajulus where the sacculi are less extensive. (See Fig. 78). There are also short muscle fibers attaching the latter to the lateral extensions of the central tendon, mandibular apomedes and posterior tentorial processes, and probably numerous secondary attachments which I have overlooked. The secondary, peripheral chambers which communicate with the

central one, are most numerous in the anterior part of the sacculi but are also clearly distinguishable at the sides, while many irregular recesses of the body cavity penetrate between the walls of the latter and may contain leucocytes which I have observed especially well in Fontaria (See Fig. 81). As regards the tissue composing the walls and partitions of the sacculi, there is nothing to suggest that it is genetically related to the columnar epithelium of the labyrinths which assumes an infundibular shape and ends very abruptly at the point where the two structures unite. In places the tissue is epitheloid but always syncytial with a more or less recticular cytoplasm which takes a much lighter stain than that of the labyrinth cells. Both externally and internally, the walls are lined by an extremely flat membranous layer which presents small dark nuclei at wide intervals apart and might thus be looked upon as a squamous epithelium. Often strands from this layer may be seen traversing the cytoplasm at oblique angles. The epitheloid appearance, above mentioned, is due to the occurrence of larger, somewhat elliptical nuclei at fairly close intervals within the cytoplasm, but usually these are quite diffuse and far apart. It is reasonable to suppose that the cytoplasm and larger nuclei, however few they may be, constitutes the parenchyma of the sacculi while the peripheral membranous layers are stromatic and serve largely to protect and strengthen the former. But in many places the cytoplasm suggests blood plasma and might therefore be interpreted as haemocoelomic recesses between the peripheral layers, which would then constitute the intrinsic tissue of the sacculi. (See Fig. 81). In the central chambers of Scytonotus I have often seen what is apparent-

ly excretory matter in the form of large and small globules and granules, but have not observed any definite content within the chambers of the other genera. The general shape, position and structure of the sacculi would make it seem very probable that they serve as nets or filters for collecting excretory matter from the blood in its flow caudad from the region of the brain. (See Figs. 78 to 82).

C. Summary.

1. In all four genera the tubular glands present the same general plan of structure and consist of two morphologically distinct parts; labyrinth and sacculus. The labyrinth is a more or less coiled tube comprising a descending ramus which opens at the base of the interstipital groove of the gnathochilarium and runs caudad in the trunk for a greater or less distance at each side of the digestive tract, and an ascending ramus continues with the descending and extending cephalad to the posterior part of the head where it opens into the sacculus. The sacculus is an irregularly pyramidal, thin walled structure consisting of a central chamber with the opening of the labyrinth at its caudal end and a large number of peripheral chambers communicating with the central one.

2. The labyrinths are of even diameter throughout except for a short distance behind their interstipital openings where they are distinctly narrower than elsewhere. In Parajulus they extend farther caudad than in the other genera while their ascending and descending rami are clearly apposed and invested by a com-

mon basement membrane. But in the Polydesmoids they end posteriorly at the cardiac valve where they are greatly coiled and the two rami are distinctly separate at all points. The ascending rami of Fontaria are much more coiled than in Scytonotus and Orthomorpha.

3. Near the interstipital openings, the labyrinths are lined by a thin chitinous intima and invested by a cuboidal layer, but present a columnar epithelium and a cuticular border throughout the remainder of their course. In Fontaria the cells are relatively higher than in the other genera, but, in all, the nuclei are centrally situated and the cytoplasm, homogeneous or slightly granular and deeply stainable.

4. The cuticular border shows a prominent basilar membrane but its processes are not clearly definable in any of my preparations. It may be cast off at once by a fairly extensive area of the epithelium.

5. The substances discharged by the epithelium are probably fluid to a large extent and take the form of large clear vacuoles in the distal half or third of the cells which contrast markedly with the dense basal cytoplasm.

6. The epithelium rests upon a prominent, non-cellular basement membrane which is penetrated at various levels by tracheae that apparently have end cells between the basal half or two thirds of the epithelial cells.

7. The sacculi of Parajulus are relatively smaller than in the Polydesmoids, but in all four genera are connected with each other below the oesophagus and held in place by attachments to the

dorsal wall of the oesophagus, to apodemes arising near the bases of the antennae, to the lateral extensions of the central tendon, to the posterior processes of the tentorium in Parajulus or the premandibular apodomes in the Polydesmoids.

8. The walls of the sacculi comprise a syncytium with clear, more or less, reticular cytoplasm and irregularly distributed nuclei, which is invested both internally and externally by a thin membranous epithelium containing very small dark nuclei. It is possible that what I have recognized as cytoplasm may be blood plasma filling haemocoelomic recesses.

9. The structure of the sacculi strongly suggests an excretory function for the tubular glands.

10, Situated ventro-laterally in the head of Orthomorpha are a pair of glands consisting of a loose aggregation of alveoli which open by slender chitinous ducts into the bases of the interstipital grooves. The epithelium of the ducts is flat but directly continuous with the alveolar cells which are very similar to the anterior and posterior salivary gland cells. These glands probably produce a watery secretion which I have seen discharged from the interstipital grooves over the Diplopod's food before the latter is consumed. Similar glands are present in Parajulus but I have been unable to observe their ducts. The term, maxillary or gnathochilarial glands might be appropriately applied to these structures.

4. Malpighian Tubules.

The Malpighian tubules of Diplopods were recognized by the

earlier authors but were first demonstrated to be urinary organs by Leydig (1866) and especially Plateau (1877) who obtained uric acid crystals from their tissue by the acetic acid test. Plateau also found that they open laterally into the digestive tube at the point of junction between mid and hindguts in both Julus and Glomeris, but claims that their number is four in the former but two in the latter where their caliber is relatively large and their cells relatively small. Rossi (1902) and Krug (1907), however, describe them as only a single pair for Julus and all subsequent investigators are agreed that this number is constant throughout the class. As I have already intimated, they have been found to insert at the junction of mid and hindgut in Julus, Craspedosoma and Polyxenus but at a considerable distance caudad of the pyloric valve in Polydesmus. Krug (1907), Effenberger (1909) and Wernitzsch (1910) represent them as comprising a simple cuboidal or low columnar epithelium and as variable in caliber throughout their greatly coiled course but do not refer to their distribution within the trunk in precise terms. In Polyxenus lagurus, Bode (1877) describes the tubules as inserting into the hindgut at both its anterior and posterior extremities, while Heathecote (1890) claims that they insert only at the pyloric valve, but further notes that they run caudad along the sides of the hindintestine to points laterad of the anus where each forms a double coil and thence proceed cephalad with a greatly reduced diameter. He does not explain what becomes of them in the anterior part of the trunk, though he refers to a flat cellular membrane fused with the hypodermis posteriorly which completely in-

vests the entire hindgut and the tubules as far forward as the pyloric valve and which is penetrated by the small ascending rami of the latter in their anterior course Reinecke (1910) mentions the membrane, and describes the tubules throughout their entire distribution. He agrees with Heathecote in regard to their posterior disposition but finds that the small rami continue cephalad until they reach the cardiac valve, whereupon they turn caudad as descending rami and end in another pair of double coils at the level of the pyloric valve. It will thus be seen that each tubule here comprises a thick, proximal descending ramus, a double coil, a slender ascending ramus, a slender distal descending ramus and a distal double coil. Issajew (1911) refers to the proximal parts of the tubules in Polyxenus lucidus as very thick and greatly coiled but does not state whether the coils are near the pyloric valve or the rectum. Both Heathecote and Reinecke figure cross sections of the proximal descending and ascending rami which agree in showing a very small central lumen invested by a thick ring of cytoplasm containing a single nucleus. This is a wide departure from the many celled condition encountered in the other genera and, according to Veneziani (1904) would indicate a high degree of specialization, since the latter considers the typical Diplopod tubule with its many small but distinct cells as more primitive than the typical insect with its larger, fewer and more confluent cells. Bruntz (1903) claims to have demonstrated that the Malpighian tubules of Julus and Glomeris are excretory but does not specify as to how they reacted toward his vital stain injections.

A. Distribution and Structure.

I have already referred to the Malpighian tubules as inserting at the junction of mid and hindguts in Parajulus, and between the anterior and middle regions of the intestine in the Polydesmoids. Their distribution in the trunk, however, is fundamentally similar in all four genera but quite different from that of Polyxenus. From the lateral openings, proximal ascending rami follow a more or less tortuous course ventro-laterad of the digestive tube as far as the anterior part of the first trunk segment, then turn about and, as distal descending rami, extend caudad to the third, second or first segment from the anal where they end blindly. In Parajulus the proximal rami have an average diameter of 28 microns and are only moderately coiled in their anterior course. Just beyond their insertions they are symmetrically disposed; the left ramus first extends caudo-ventrad, forms a loop beneath the gonads and then proceeds cephalad, while the right forms a smaller loop on the dorsal side of the intestine a short distance posterior to the pyloric valve before beginning its ascent. The transition between ascending and descending rami is here marked by a very sharp bending of the tubules upon themselves, and an abrupt decrease in diameter to 15 microns. Caudad, the descending rami follow a course which parallels that of the ascending and at most oesophageal and midintestinal levels lie mediad of the latter, but at points a short distance anterior to the pyloric valve they suddenly acquire a diameter of 28 microns and thence pursue a relatively straight course lateral to the mid and hindintestines. As I have intimated, the descending rami

end blindly, laterad or dorso-laterad of the posterior region of the hind intestines, and in the first, second or third segment anterior to the anal. A small group of muscle fibers originating laterally on the anterior margin of the anal segment insert on the basement membrane at their blind ends and by contraction and expansion can thus alter the relative positions of the latter. In a number of individuals examined, the right descending ramus was resolved in a small loop on the dorso-lateral wall of the hindgut midway between its two extremities, but all the other conditions to which I have referred showed only insignificant variations. (See Fig. 84, I.). The disposition of the tubules in Scytonotus and Orthomorpha are very much alike and simpler than in Parajulus. Their diameter, which averages 25 microns, is about the same in both ascending and descending rami and there are no conspicuous asymmetries at any points throughout their moderately coiled course. Near their insertion in adult Orthomorphae the descending rami form distinct loops on the ventro-lateral wall of the midgut just above the pyloric valve, but these are apparently lacking in immature Orthomorphae and adult Scytonoti. Within the first four segments of the trunk, both ascending and descending rami are much more coiled than elsewhere, and the transitions from the former to the latter are not so clearly defined as in Parajulus, but throughout the extent of the tubules, the secondary coils are more pronounced in the mature than in the immature Orthomorphae. In Scytonotus, the blind ends of the descending rami have the same sort of muscular attachment to the anterior margin of the anal segment that obtains in Parajulus. I believe that the same condition is present in Orthomorpha as well, but both my sectioned

end blindly, laterad or dorso-laterad of the posterior region of the hind intestines, and in the first, second or third segment anterior to the anal. A small group of muscle fibers originating laterally on the anterior margin of the anal segment insert on the basement membrane at their blind ends and by contraction and expansion can thus alter the relative positions of the latter. In a number of individuals examined, the right descending ramus was resolved in a small loop on the dorso-lateral wall of the hindgut midway between its two extremities, but all the other conditions to which I have referred showed only insignificant variations. (See Fig. 84, I.). The disposition of the tubules in Scytonotus and Orthomorpha are very much alike and simpler than in Parajulus. Their diameter, which averages 25 microns, is about the same in both ascending and descending rami and there are no conspicuous asymmetries at any points throughout their moderately coiled course. Near their insertion in adult Orthomorphae the descending rami form distinct loops on the ventro-lateral wall of the midgut just above the pyloric valve, but these are apparently lacking in immature Orthomorphae and adult Scytonoti. Within the first four segments of the trunk, both ascending and descending rami are much more coiled than elsewhere, and the transitions from the former to the latter are not so clearly defined as in Parajulus, but throughout the extent of the tubules, the secondary coils are more pronounced in the mature than in the immature Orthomorphae. In Scytonotus, the blind ends of the descending rami have the same sort of muscular attachment to the anterior margin of the anal segment that obtains in Parajulus. I believe that the same condition is present in Orthomorpha as well, but both my sectioned

and dissected material failed to verify this. (See Figs. 81 and 84, 2 and 3.). The tubules of Fontaria are quite symmetrical, but greatly coiled at all points anterior to the pyloric valve. From their insertions the ascending rami run ventro-cephalad to the ventral side of the midgut as straight tubes with a diameter of 120 microns but in their coiled ascent beneath the midgut they gradually decrease to about 40 microns. A short distance caudad of the cardiac valve, each ramus enters the posterior end of an elongated, subcylindrical body which lies ventro-laterad of the digestive tube and extends forward as far as the third trunk segment. These bodies comprise densely massed coils of the ascending rami interspersed with large tracheal branches from a pair of trunks which have been recognized for a long time in Diplopods as originating in the fifth segment and distributing to the head. They are invested by a squamous epithelium comprising large, somewhat branched cells with dense cytoplasm and large reniform nuclei, and might be appropriately named the anterior tubular complexes. Within the complexes the ascending rami show a diameter of about 55 microns but after leaving the latter at their anterior ends this becomes reduced to 35. From this point, on to the first segment of the trunk the rami continue as greatly coiled tubes which thence proceed caudad without showing any appreciable changes in disposition or caliber until they reach the pyloric valve. Here they undergo a rather abrupt reduction to 25 microns in diameter, follow an almost straight posterior course laterad of the intestine and end precisely as in Parajulus and Scytonotus. (See Figs. 18 and 84,4.).

Except in the large proximal parts of the ascending rami in

Fontaria where the cells are long and narrow with an average height of 25 microns and basally situated, elliptical nuclei (See Fig. 85, D.) the epithelium of the urinary tubules is either cuboidal or low columnar and the nuclei round and centrally situated. In Parajulus the cells of the ascending rami and large posterior parts of the descending number about 14 to the cross section and have a height of from 4 to 8 microns, while those of the small parts of the descending number about 6 or 7, and their height rarely exceeds 3 microns. The number in Scytonotus and Orthomorpha averages 11, and the height 4 microns, but in Fontaria the coiled parts of the ascending and descending rami have a number of from 30 to 40, and a height of 8 microns. Within the tubular complexes both number and height slightly exceed these figures while in the small posterior part of the descending rami they are about the same as in the entire tubule of Scytonotus and Orthomorpha. (See Fig. 84, 1, 2, 3, and 4.). Aside from the differences just mentioned, the epithelia are very similar in all four genera and strikingly like the labyrinth of the tubular glands as regards the presence and structure of the cuticular border, the texture and staining reactions of the cytoplasm, the accumulation of excretia as vacuoles in the distal half or third of the cells, and the relationship between epithelium and tracheae. (See Fig. 86 A. and B.). This close similarity in so many respects might be accepted as additional evidence in favor of regarding the labyrinths as excretory. Leaving relative size out of the question, the cells of the tubules might be said to differ from those of the labyrinths in presenting a rounded

rather than a polygonal outline in surface view, in the predominance of the round, rather than the elliptical nuclei, and in the somewhat darker and often more uniform staining of the cytoplasm. At their points of insertion, the prominent, non-cellular basement membrane of the tubules is distinctly continuous with that of the intestinal epithelium and the cells gradually assume the character of the intestinal cells adjacent to the openings. Because of this gradual transition from one kind of cell to another, the chitinous intestinal intima, which extends a short distance into the canal of the tubules, seems to merge imperceptibly with the cuticular border. (See Fig. 85. A, B, C and D). In Fontaria I have observed a few slender longitudinal muscle fibers lying along the walls of the tubules near their points of insertion. These arise as branches from the longitudinal fibers as in Cryptops according to Balbiani (1890), but they are much less prominent than in the latter and probably do not extend very far distad. (See Fig. 85, D). I have found no evidences of muscle fibers following a spiral or branched course along the walls of the distal parts of the Malpighian tubules such as have been observed in Orthoptera and Coleoptera by Léger and Duboscq (1899) and Veneziani (1904).

B. Summary.

1. The Malpighian tubules in all four genera are ventrolateral of the digestive tract throughout the greater part of their extent, and consist of proximal ascending rami which turn upon themselves in the first trunk segment and continue caudad as descending rami. In Parajulus, Scytonotus, Fontaria, and probably

Orthomorpha, they end blindly a short distance cephalad of the anal segment, but are attached by muscle fibers to the anterior margin of the latter.

2. In Parajulus, the tubules distribute asymmetrically near their point of insertion and the anterior parts of the descending rami have a distinctly smaller caliber than the posterior parts and ascending rami.

3. In Scytonotus and Orthomorpha the tubules are symmetrical and subequal in diameter throughout. Except in the anterior region of the trunk, they follow a straighter course than in Parajulus, but in immature Orthomorphae the secondary coils of the tubules are less pronounced than in the adult.

4. At all points anterior to the pyloric valve, both the ascending and descending rami are very intricately coiled in Fontaria, and of fairly constant caliber, but near their insertions, the ascending rami are straight and of a much greater diameter than elsewhere. Ventro-laterad of the cardiac valve, the latter enter into the composition of a pair of elongated, subcylindrical bodies which are invested by a squamous epithelium comprising large cells with reniform nuclei, and which, together with the closely massed coils of the tubules, contain large tracheal branches arising from a pair of trunks that extend forward from the fifth segment and distribute to the head. I have designated these structures the anterior tubular complexes. The posterior parts of the descending rami are of relatively small diamater and follow an almost straight course.

5. The epithelia of the Malpighian tubules are cuboidal or low columnar in all four genera, except in the proximal parts of

the ascending rami of Fontaria where the cells are high columnar.

6. In all but a few unimportant respects the cells of the tubules are closely similar to those of the labyrinths of the tubular glands. This is additional evidence in favor of regarding the latter as excretory organs.

7. At the points of insertion there is a gradual transition from the tubular to the intestinal epithelium, and the intima gradually merges with the cuticular border of the tubules.

8. In Fontaria branches from the longitudinal muscle fibers of the intestine continue along the walls of the proximal parts of the ascending rami for a short distance, but I have found no further indication of a muscularis associated with the Malpighian tubules.

5. Anal Glands.

Vom Rath (1890) notes that the female Polydesmus has the habit of tipping the earth which she later uses in constructing a nest for her eggs many consecutive times with her anus, and concludes, that, in so doing, she gives off a secretion from the latter which serves to cement the particles of earth together. Rossi (1902) overlooks this observation in ascribing a nest-building function to the tubular glands in Julus and also fails to explain why structures with a function peculiar to one sex should be equally well developed in both. Later Effenberger (1909) observed refractive droplets of secretion being released by female Polydesmi during the nest building process, and also discovered a large glandular mass of tissue lying dorsad of the hindgut near its posterior extremity and opening dorso-laterally into the caudal part of the rectum by a pair of very small, in-

distinct ducts. He further describes the glandular tissue as diffuse, histologically similar to the anterior and posterior salivary glands, and extending an appreciable distance cephalad from the anal segment, but was apparently unable to obtain sections showing much histological detail. Since he finds this structure present only in the females, Effenberger, with good reason, regards it as the source of the nest-building secretion. For Craspedosoma, Wernitzsch refers to a pair of small trabecular glands lying laterad of the rectum and opening into it ventro-laterally by a pair of slender ducts. Though present in both sexes, he recognizes these as homologues of the much larger glandular mass of Polydesmus, but claims that they have undergone reduction and are functionally supplemented by a pair of tubular silk glands which open at the tip of the mucro or posterior extension of the tergite of the anal segment. In no other instances, that I am aware of, have anal glands or structures analogous to them been observed and described in Diplopods.

In mature or nearly mature female Scytonoti, Orthomorphae and Fontaria, I have found structures which correspond very closely with Effenberger's rather incomplete description of the anal glands in Polydesmus. They are relatively similar in all three genera, distinctly paired and situated dorso-laterad of the hindgut. Caudad, above the rectum, they are united, and cover its entire dorsal surface, but in the anterior part of the anal segment where the posterior region of the intestine arches dorsad, they separate and extend cephalad as far as the fourth segment anterior to the anal, thus describing a U or V, when seen in

dorsal view. (See figs. 2, 3 and 4). The ducts are essentially like those of the anterior and posterior salivary glands, are centrally situated in each gland, and run parallel with their long axes. They give off numerous collateral branches throughout their course, and open laterad into the posterior part of the rectum at the level where the rectal epithelium and hypodermis unite. (See Figs. 61 and 87). As in the anterior salivary glands, the glandular tissue is interrupted at the points where the intestinal and rectal suspensory muscles pass to their origins on the anterior margin of the anal segment.

A. Ducts.

In Fontaria my material does not include any sections through the anal glands and consequently my histological observations are limited entirely to Scytonotus and Orthomorpha. The ducts in both these genera are almost identical, and are lined throughout by a chitinous intima continuous with that of the rectum but much thinner within the tissue of the glands than elsewhere. As in the anterior salivary glands, the ducts enter the latter almost immediately distad of their openings, and their epithelium, which is confluent with that of the rectum and hypodermis and proximally cuboidal, becomes thin and squamous throughout the remainder of its extent. Conspicuous bundles of small tracheae lie close along the walls of the ducts, and branches from these are apparently intracellular within the glandular parenchyma, but I have observed nothing which would suggest that the ducts end intracellularly. The lumen of the latter often

contains a homogeneous or slightly fibrous secretion, which stains an intense blue under Mallory, and thus resembles the secretion of the posterior salivary glands. (See Figs 87 and 88).

B. Gland Cells.

The gland cells in both Scytonotus and Orthomorpha are very large with poorly defined boundaries and relatively small, elliptical, or somewhat irregular nuclei. Their cytoplasm is, for the most part, finely reticular, but may appear distinctly vacuolated in places. It always takes a deep, uniform stain and, whether fixed with Flemming's or Bouin's fluid, appears bright blue under Mallory. Almost every cell that I examined contains one or two structures made up of radially arranged spongioplasmic fibrils like those which I previously mentioned as occurring in the cells of the anterior salivary glands of Orthomorpha. Here and there, the nuclei occupy the center of these bodies, but usually the latter take the form of round clear vacuoles, and in places, where the bodies are close together, the radial spongioplasmic fibrils interconnect. There are, however, no indications that the clear central vacuoles are continuous as intracellular canals, since they do not recur in serial sections, and appear circular throughout the tissue of the glands, regardless of sectioning planes. (See Fig. 88, A.).

Occurring as dorsal evaginations from the anterior part of the rectal epithelium in adult males and sixth and seventh instar immature Orthomorpha of both sexes, I have observed a variable number of small, deeply stained glandular bodies comprising large cells, relatively small, elliptical nuclei, and

a restricted lumen lined by a thin chitinous intima. In a sixth instar male, I identified only two of these bodies, but recognized four in a seventh instar female and adult male. These correspond very closely to the reduced anal glands which Wernitzsch found in both sexes of Craspedosoma, and it is not unlikely they are anlage of the anal glands which reach their full development only in the mature female Orthomorphae. (See Fig. 88 B.).

C. Summary.

1. Anal glands, probably similar to those of Polydesmus, occur in the adult females of Scytonotus, Orthomorpha and Fontaria.

2. They are similar in all three genera, paired and dorsolateral to the rectum and posterior region of the intestine. Over the former, they are contiguous, but are separated from each other anteriorly and extend as far forward as the fourth segment from the anal.

3. The ducts are centrally situated in each gland, give off numerous collateral branches throughout their course, and open laterad at the posterior extremity of the rectum. They are lined by a chitinous intima continuous with the rectal and their epithelium is proximally confluent with that of the rectum and hypodermis, but within the glandular tissue both intima and epithelium are reduced to thin layers. As in the anterior and posterior salivary glands, there are no indications of intracellular endings.

4. In Scytonotus and Orthomorpha, the gland cells are very

large with relatively small nuclei and finely reticular cytoplasm which stains a bright blue under Mallory. Bodies consisting of spongioplasmic fibrils radially arranged about a clear central vacuole are quite evenly distributed throughout the cytoplasm.

5. In mature males and immature sixth and seventh instar Orthomorphae of both sexes are a number of dorsal, glandular evaginations from the anterior part of the rectal epithelium which may be anlage of the fully developed anal glands in the adult females.

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Note: x = papers directly related to Diplopoda.

VII. LEGEND

I. Figures.

Figs. 1, 2, 3 and 4. Entire digestive tracts as seen from a dorsal view, with head and trunk segments diagrammatically outlined and suspensory muscles omitted. Fig. 1. = Parajulus, adult, 53-segmented female, x 5. Fig. 2. = Scytonotus, adult female, x 10. Fig. 3. = Orthomorpha, adult female, x 10. Fig. 4. = Fontaria, adult male, x 5.

Fig. 5. Dorsal view of skeletonized pharynx of Parajulus, semi-diagrammatic, x 60. The dorsal pharyngeal eminence, premandibular masticatory plates and prepharynx are covered by the dorsal wall of the pharynx, and the premandibles are spread laterad farther than normal. (1) and (2) = Openings of lateral and medial anterior salivary ducts. (3) = Attachment of pars transversalis tentorii to exoskeleton caudad of base of Antenna.

Fig. 6. Sagittal section thru head of Parajulus, adult male, x 62½. (1) = Dorsal pharyngeal wall cut at junction of median anterior lamina and median anterior laminette. (2) = Masticatory plate of premandible cut tangentially and showing pores. (3) = Point of junction between pharynx and oesophagus. Mallory - Bouin's - 10 microns.

Fig. 7. Sagittal section thru head of Orthomorpha, adult male, x 62½. (1) = Dorsal pharyngeal wall cut closer to medial plane than in Fig. 6. and including the lateral part of the dorsal pharyngeal eminence. The ventral pharyngeal wall is cut more laterad than in Fig. 6. (2) = Point of junction between pharynx and oesophagus. Mallory - Bouin's - 10 microns.

Fig. 8. Transverse (horizontal) section thru head of Parajulus,

nearly mature female. A.1.= Section thru entire head at level of prepharynx, x 62½. A.2.= Section thru middle third of hypostoma showing interstipital grooves, x 125. B.= Part of premandibular masticatory plate showing sensory cells and pits, x 300. C.= Prepharynx showing relationship of pharyngeal epithelium to corpus, x 300. (1)= Specialized (possibly sensory) pharyngeal cells. (2)= Distal parts of cells extending into sensory pits. (3)= Mandibular nerve. Haemalum, eosin - Bouin's - 8 microns.

Fig. 9. Transverse (horizontal) section thru head and first trunk segment of Orthomorpha, nearly mature female. Anterior part of section cut at a more ventral and posterior part at a more dorsal level than that of Fig. 8.A.1. A.= Section cutting ventral pharyngeal wall at level of prepharynx, x 62½. B.= Prepharynx from a section slightly dorsal to that of Fig. 9.A., x 300. (1)=Tergite of first trunk segment. Haemalum, eosin, Orange G. - Bouin's - 10 microns.

Fig. 10. Sagittal section thru dorsal pharyngeal eminence of Fontaria, x 125. Haemalum, eosin, Orange G. - Bouin's - 10 microns.

Fig. 11. Skeletonized prepharynges and tentoria, dorsal view, x 60. A.= Parajulus. B.= Orthomorpha. C.= Scytonotus. D. = Fontaria (most of tentorium omitted). (1)= Flat surface continuous with pharyngeal intima. (2)= Central tendon omitted.

Fig. 12. Shape of the oesophageal lumen of Parajulus at different serial levels within the head, x 125. A.= Cross section of oesophagus at its anterior extremity. B.= Cross section below brain. C.= Cross section a short distance cephalad of pseudocciput. D. = Cross section at level of pseudocciput. Haemalum,- Bouin's - 7 microns.

Fig. 13. Cross section thru the midregion of the oesophagus of Parajulus showing differentiation of chitinous intima into ental and ectal zones, x 300. Posterior salivary glands included. Mallory - Bouin's - 5 microns.

Fig. 14. Cross section thru the third trunk segment of a nearly mature male Parajulus, x 140. Ventral part of segment omitted. Haemalum, eosin - Bouin's - 8 microns.

Fig. 15. Enlarged view of oesophagus shown in Fig. 14., x 630. The pigment granules are here very abundant in the oesophageal epithelium. Haemalum, eosin, Bouin's - 8 microns.

Fig. 16. Cross section thru posterior fourth of oesophagus of a nearly mature male Parajulus showing the lumen dilated and the rugae suppressed, x 140. The chitinous intima is pulled away from the underlying epithelium thruout the greater part of its extent. Haemalum, eosin,- Bouin's - 8 microns.

Fig. 17. Cross section thru posterior fourth of oesophagus of a nearly mature female Orthomorpha, showing posterior salivary and tubular glands and Malpighian tubules, x 300. Mallory - Bouin's - 10 microns.

Fig. 18. Cross section thru the posterior fourth of the oesophagus of an adult male Fontaria, x 125. Posterior salivary and tubular glands and Malpighian tubules included but anterior tubular complexes omitted. Benda's iron haematoxylin - Flemming's - 7 microns.

Fig. 19. Surface view of the oesophageal muscularis from the anterior part of the oesophagus of Parajulus showing the disposition of the circular muscle fibers, x 600. Haemalum, eosin -Bouin's - 8 microns.

Fig. 20. Longitudinal section thru the cardiac valve of Parajulus, adult, x 300. Benda's iron haematoxylin - Bouin's - 6 microns.

Fig. 21. Longitudinal section thru the cardiac valve of Scytonotus, adult, x 300. Haemalum - Bouin's - 7 microns.

Fig. 22. Longitudinal section thru the cardiac valve of Orthomorpha, 6th instar, 7 mm. 18-segmented male, x 300. (1)= Continuation of oesophageal intima with peritrophic membrane. Haemalum - Bouin's - 8 microns.

Fig. 23. Longitudinal section thru the cardiac valve of Fontaria, adult, x 300. (1)= Basement membrane obliquely cut and presenting a distinctly fibrous appearance. Mallory - Bouin's - 7 microns.

Fig. 24. Midintestinal epithelium from a cross section thru the midgut of an adult Parajulus showing the peritrophic membrane in process of formation, x 350. Haemalum - Bouin's - 7 microns.

Fig. 25. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Scytonotus showing the peritrophic membrane in a later stage of formation than that of Fig. 24 ., x 350. The midgut is here more expanded and the epithelium lower than in the preceding figure. (1) = Brush border which has apparently reappeared after the peritrophic membrane became detached from the cells underlying the former. Mallory - Bouin's - 7 microns.

Fig. 26. Midintestinal epithelium from a longitudinal section thru the midgut of a 6th instar Orthomorpha showing mature cells in very active secretion of peritrophic membrane, x 600. Haemalum - Bouin's - 8 microns.

Fig. 27. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Fontaria showing the formation of the peritrophic membrane, x 350. Benda's iron haematoxylin - Flemming's

- 7 microns.

Fig. 28. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Parajulus showing cells in typical brush border stage, x 400. A.= Epithelium in usual state of contraction. B.= Epithelium from region where midintestinal lumen is distended. C.= Unusually elongated and widely separated brush border processes. Mallory - Bouin's - 7 microns.

Fig. 29. Midintestinal epithelium from a cross section thru the midgut of an adult Parajulus, x 600. (1)= Secretion being discharged in small masses. Acid thionin - Hermann's - 4 microns.

Fig. 30. Midintestinal epithelium from a cross section thru the midgut of an adult Scytonotus showing cells in typical brush border stage, x 600. Secretory granules, S.G., very distinct. Benda's iron haematoxylin - Flemming's - 7 microns.

Fig. 31. Midintestinal epithelium from a cross section thru the midgut of an adult Orthomorpha showing cells in typical brush border stage, x 600. (1)= Distal, secretory parts of cells very distinctly vacuolated. Haemalum, eosin, O.G. - Bouin's -10 microns.

Fig. 32. Midintestinal epithelium from a cross section thru the midgut of an adult Fontaria showing cells in typical brush border stage, x 600. (1)= Secretion being discharged in small quantities. Haemalum, - Bouin's - 7 microns.

Fig. 33. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Parajulus showing cells in an early stage of discharge, x 600. (A)= Secretion becoming fully elaborated at distal extremity of mature cell. (B.B.1.)= Brush border still adherent to mature cell. (B.B.2.)= Brush border adherent to secretion sphere which has been cast off from discharging cell. Haemalum-Bouin's - 7 microns.

Fig. 34. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Parajulus showing cells in an advanced state of discharge and the formation of a new brush border (B.B.F.), x 600. Benda's iron haematoxylin - Flemming's - 5 microns.

Fig. 35. Midintestinal epithelium from a cross section thru the midgut of an adult Parajulus showing cells in an advanced state of discharge, x 600. This preparation shows the stages in the elaboration of the secretory granules (S.G.(1),(2) + (3)) very clearly. Acid thionin - Flemming's - 5 microns.

Fig. 36. Midintestinal epithelium from a cross section thru the midgut of an adult Parajulus showing cells in an advanced state of discharge, x 600. (1)= Secretory content of discharging cells which in this preparation takes the form of reddish vacuoles. Benda's iron haematoxylin, eosin, O.G. - Bouin's - 8 microns.

Fig. 37. Entire cross section thru a contracted region of the midgut of a nearly mature male Parajulus showing epithelium in an active state of discharge, x 140. Section taken thru anterior third of midgut. Haemalum, eosin, O.G. - Bouin's - 8 microns.

Fig. 38. Midintestinal epithelium from an adult Scytonotus showing cells in an active state of discharge. A. Epithelium from a longitudinal section showing secretory granules in discharging cells very distinctly, x 600. Acid thionin - Flemming's - 5 microns. B. Epithelium from a cross section showing discharging cells,(1) with a dark, homogeneous, mucoid content, x 300. Haemalum - Flemming's - 7 microns.

Fig. 39. Midintestinal epithelium from a cross section thru the midgut of an adult Orthomorpha showing cells in an active state of discharge, x 600. Benda's iron haematoxylin - Flemming's - 7 microns.

Fig. 40. Midintestinal epithelium from a longitudinal section thru the midgut of an adult Fontaria showing cells in an advanced state of discharge, x 600. (1)= Secretory content of discharging cells in the form of clear vacuoles. Benda's iron haematoxylin - Flemming's - 7 microns.

Fig. 41. Midintestinal epithelium from the posterior extremity of the midgut of an adult male Parajulus which was starved for 13 days, x 400. (1)= Ental stratification of elongated cells. Haemalum - Bouin's -5 microns.

Fig. 42. Midintestinal epithelium from a region of the midgut just anterior to that shown in Fig. 41. and of the same specimen, x 600. Haemalum - Bouin's - 5 microns.

Fig. 43. Midintestinal epithelium representing the typical condition met with in the anterior nine tenths of the midgut of a nearly mature female Parajulus starved for 42 days, x 600. Benda's iron haematoxylin - Bouin's - 5 microns.

Fig. 44. Midintestinal epithelium from the posterior extremity of the midgut of the same specimen as represented in Fig. 43., x 600. (1)= Clumps of small, rounded cells with picnotic nuclei. Haemalum - Bouin's - 5 microns.

Fig. 45. Midintestinal epithelium from a level just anterior to the posterior extremity of the midgut of an adult female Parajulus in hibernation, x 600. Haemalum - Bouin's - 7 microns.

Fig. 46. The Polycystid Gregarine, Stenophora julipusilli - Leidy, a common parasite of the midgut of Parajulus venustus. A. Midintestinal epithelium of Parajulus showing various intracellular stages within the mature host cells, x 300. B. A mature trophozoite of the elongated type, x 250. (1)= Early sporozoite stage. (2)= Later sporozoite stage. (3)= Early trophozoite stage (elongated

type). (4)=Later trophozoite stage (round type). (5)= Protomerite. (6)= Deutomerite. (7)= Pore. Haemalum - Bouin's - 7 microns.

Fig. 47. An apparently unidentified Polycystid Gregarine of frequent occurrence within the midgut of Fontaria virginiensis brunnea. A. Late intracellular trophozoite stage with epimerite and protomerite still within the cytoplasm of the host cell, x 300. B. Trophozoite free in the lumen, x 300. (1)= Late intracellular trophozoite. (2)= Epimerite. (3)= Protomerite. (4)=Deutomerite. Benda's iron haematoxylin - Flemming's - 7 microns.

Fig. 48. Surface view of midintestinal muscularis of Parajulus, x 600. Mallory - Bouin's - 6 microns.

Fig. 49. Epitheloid cells from an oblique section thru the midgut of Parajulus showing the relationship of the former to the midintestinal tracheae, x 600. Benda's iron haematoxylin - Bouin's- 6 microns.

Fig. 50. Longitudinal section thru the pyloric valve of an adult Parajulus, x 300. Haemalum - Bouin's - 7 microns.

Fig. 51. Longitudinal section thru the pyloric valve of an adult Orthomorpha, x 300. Benda's iron haematoxylin - Flemming's - 6 microns.

Fig. 52. Longitudinal section thru the pyloric valve of an adult Fontaria, x 300. (1)= A small, inner midintestinal longitudinal muscle fiber branching off from a bundle of outer midintestinal longitudinals. Mallory - Bouin's - 7 microns.

Fig. 53. Cross section thru the cephalic portion of the anterior region of the intestine of an adult Parajulus showing rounded, irregular rugae, x 125. Haemalum - Bouin's - 7 microns.

Fig. 54. A. Cross section thru the anterior region of the intestine of an adult Parajulus at a level just anterior to the

posterior region, x 125. Haemalum - Bouin's - 7 microns. B. Cross section thru the posterior region of an adult Parajulus, x 125. Mallory - Bouin's - 7 microns.

Fig. 55. Spiniferous cells from a longitudinal section thru the anterior region of the intestine of an adult Orthomorpha, x 600. (1)= Tip of spine penetrating peritrophic membrane. (2)= Minute fibers attaching bases of spines to circular muscle fibers. Benda's iron haematoxylin - Flemming's - 6 microns.

Fig. 56. Intestinal epithelium from a cross section thru the posterior region of an adult Orthomorpha, x 600. Mallory-Bouin's - 10 microns.

Fig. 57. Intestinal epithelium from a cross section thru the middle region of an adult Fontaria, x 125. (1)= Epithelium cut tangentially. Lyon's blue - Bouin's - 7 microns.

Fig. 58. Intestinal epithelium from a longitudinal section thru the posterior region of an adult Fontaria, x 600. Haemalum, eosin, O.G. - Bouin's - 10 microns.

Fig. 59. Cross section thru the middle region of the intestine of an adult Scytonotus at a level just caudad of the openings of the Malpighian tubules and showing an opening of one intestinal gland into the intestinal lumen, x 125. Haemalum - Flemming's - 7 microns.

Fig. 60. Sagittal section thru the posterior extremity of the trunk of an adult Parajulus showing the posterior region of the intestine and rectum, x 62½. The section is too far laterad of the median plane to include the anus. Mallory - Bouin's - 10 microns.

Fig. 61. Transverse (horizontal) section thru the posterior extremity of the trunk of an adult female Scytonotus showing the posterior region of the intestine, rectum, parts of the anal glands

and distal ends of the Malpighian tubules, x 62½. (1)= Part of anal gland near its opening. Mallory - Flemming's - 8 microns.

Fig. 62. Transition from rectal epithelium to hypodermis in Parajulus as seen in longitudinal section, x 600. Mallory - Flemming's - 10 microns.

Fig. 63. Transition from rectal epithelium to hypodermis in Orthomorpha as seen in longitudinal section, x 600. Haemalum, eosin, O.G. - Bouin's - 10 microns.

Fig. 64. Transition from rectal epithelium to hypodermis in Fontaria as seen in longitudinal section, x 300. Mallory - Bouin's 10 microns.

Fig. 65. Opening of lateral anterior salivary duct in Parajulus as seen in a transverse (horizontal) section thru the head, x 300. Mallory - Bouin's - 10 microns.

Fig. 66. Opening of medial anterior salivary duct in Parajulus as seen in a transverse (horizontal) section thru the head, x 300. Mallory - Bouin's - 10 microns.

Fig. 67. Opening of medial anterior salivary duct in Orthomorpha as seen in a sagittal section thru the head, x 300. Mallory-Bouin's - 10 microns.

Fig. 68. Tissue of anterior salivary gland in Parajulus including duct and gland cells in various secretory stages, x 600. Mallory - Bouin's - 9 microns.

Fig. 69. Tissue of anterior salivary gland in Orthomorpha, x 600. (1)= Structures comprising radiating spongioplasmic fibrils. Mallory - Bouin's - 10 microns.

Fig. 70. Tissue of anterior salivary gland in Fontaria, x 600. Haemalum, eosin, O.G. - Bouin's - 10 microns.

Fig. 71. General distribution of posterior salivary and tub-

ular glands and the openings of their ducts in relation to the hypostoma or gnathochilarium - diagrammatic - dorsal view. A.1.= Parajulus, x 20. A.2.= Parajulus, x 60. B.= Scytonotus, x 30. C.= Orthomorpha, x 30. D.1.= Fontaria, x 10. D.2.= Fontaria (right half of hypostoma), x 40. (1)= Chitinous proximal part of posterior salivary duct within ventral pharyngeal intima. (2)= Opening of posterior salivary duct. (3)= Ramification of posterior salivary duct within the glandular tissue. (4)= Posterior extremity of tubular gland at level of 19th trunk segment. (5)= Region of cardiac valve.

Fig. 72. Opening of posterior salivary duct in Orthomorpha as seen in a sagittal section thru the head, x 300. Mallory -Bouin's - 10 microns.

Fig. 73. Cross section thru posterior salivary duct of Parajulus, x 600. (1)= Attachment of muscle fibers. (2)= Attachment of tendon. Haemalum - Bouin's - 7 microns.

Fig. 74. Tissue of posterior salivary gland in Parajulus, x 600. Mallory - Flemming's - 5 microns.

Fig. 75. Tissue of posterior salivary gland in Orthomorpha, x 600. Haemalum - Bouin's - 8 microns.

Fig. 76. Tissue of posterior salivary gland in Fontaria, x 600. Haemalum - Bouin's - 7 microns.

Fig. 77. Cross sections thru the labyrinths at levels near the cardiac valve, x 600. A.= Parajulus, Haemalum - Bouin's - 8 microns. B.= Scytonotus. Mallory - Flemming's - 8 microns. C.= Orthomorpha. Mallory - Bouin's - 8 microns. D.= Fontaria. Benda's iron haematoxylin - Flemming's - 7 microns. (1)= Basal striations. (2)= Casting of cuticular border.

Fig. 78. Cross section thru the sacculus of Parajulus, x 300.. (1)= Connection of sacculus with its fellow. Mallory - Bouin's - 10 microns.

Fig. 79. Longitudinal section thru the sacculus of Scytonotus showing the infundibulum of the labyrinth, x 300. (1)= Excretory matter in central chamber. Mallory - Flemming's - 8 microns.

Fig. 80. Longitudinal section thru the sacculus of Orthomorpha, x 300. (1)= Attachment of sacculus to apodeme arising just behind base of antenna. Mallory - Bouin's - 10 microns.

Fig. 81. Tissue from longitudinal section thru the sacculus of Fontaria showing leucocytes in blood spaces or coelomic recesses, x 600. Haemalum, eosin, O.G. - Bouin's - 10 microns.

Fig. 82. Epithelium from a longitudinal section thru the labyrinth of Parajulus, x 600. A.= Cells with cuticular border. B.= Cells with ental halves filled with secretion. Mallory - Bouin's - 6 microns.

Fig. 83. Longitudinal section thru opening of labyrinth in Orthomorpha, x 300. Haemalum, eosin, O.G. - Bouin's - 8 microns.

Fig. 84. A. The distribution of the Malpighian tubules - diagrammatic dorsal view. 1.= Parajulus, x 5. 2.= Scytonotus, x 10. 3.= Orthomorpha, x 10. 4.= Fontaria, x 5. B. Sections thru levels indicated in Fig. 84.A. (a)= Cross sections thru proximal rami, x 300. (b)= Cross section thru small part of distal ramus in Parajulus, x 300. (c)= Cross section thru anterior tubular complex of Fontaria, x 125. (d)= Longitudinal section thru blind end of distal ramus in Parajulus, x 300. (1)= Openings of proximal rami into intestines.

Fig. 85. Sections thru the openings of the Malpighian tubules into the intestines, x 300. A.= Parajulus - cross section. Haemalum-

Bouin's - 7 microns. B.= Scytonotus - cross section. Haemalum, eosin - Flemming's - 8 microns. C.= Orthomorpha - cross section. Mallory - Bouin's - 8 microns. D.= Fontaria - longitudinal section. Mallory - Bouin's - 7 microns. (1)= Branches from intestinal longitudinal muscle fibers.

Fig. 86. Epithelium from a longitudinal section thru the proximal ramus of a Malpighian tubule of Parajulus, x 600. A.= Cells with cuticular border. B.= Cells with ental halves filled with secretion. Mallory - Bouin's - 6 microns.

Fig. 87. Opening of anal gland from transverse (horizontal) section thru posterior end of trunk of an adult, female Scytonotus, x 300. Benda's iron haematoxylin - Flemming's - 8 microns.

Fig. 88. A.Tissue of anal gland of an adult, female Orthomorpha, x 600. Mallory - Bouin's - 10 microns. B. Rudimentary anal glands of an adult, male Orthomorpha, x 125. Haemalum, eosin O.G. - Bouin's - 10 microns.

2. Index of Abbreviations.

A.

A.= Cephalad.

A.C.= Anterior cornua of prepharynx.

A.D.= Anterior dilatations.

A.G.= Anal glands.

A.G.R.=Rudimentary anal glands.

A.In.= Anterior region of intestine.

A.S.D.=Anterior salivary ducts.

1.=lateral. 2.= medial.

A.S.G.=Anterior salivary gland.

A.T.C.=Anterior tubular complex.

A.V.= Anal valves.

B.

B.B.= Brush border

B.B.F.=Brush border of recently matured epithelial cell.

B.L.M.=Bundle of outer midintestinal muscle fibers of Fontaria.

B.M.= Basement membrane.

BR.= Brain.

B.S.= Blood spaces.

B.T.= Basal thickenings or basilar membrane.

C.

C.= Connective tissue, blood cells, etc.

CA.= Maxillary cardines.

C.B.= Cuticular border.

C.C.= Central chamber.

C.C.R.=Cardiac cellular ring.

C.I.= Chitinous intima.

C.M.= Circular muscles.

C.S.C.= Clumps of small round cells.

C.T.= Central tendon.

C.T.L.= Lateral processes of central tendon.

C.U.C.= Peripheral chambers.

C.V.= Cardiac valve.

D.

D.= Duct.

D.C.= Old or discharging cells.

D.C.S.= Secretion sphere from discharging cells.

D.I.E.= Inferior oesophageal dilators.

D.I.PH.= Inferior pharyngeal dilators.

D.IN.= Intestinal dilators.

D.M.T.= Distal rami of Malpighian tubules.

D.L.E.= Lateral oesophageal dilators.

D.P.E.= Dorsal pharyngeal eminence.

D.RE.= Rectal dilators.

D.S.E.= Superior oesophageal dilators.

D.S.PH.= Superior pharyngeal dilators.

D.V.= Dorsal vessel.

E.

E.= Oesophagus.

E.G.C.= Gland cells in early stage of secretion.

E.M.T.= Distal end of Malpighian tubule.

EP.= Epithelium.

E.PY.= Pyloric eminence.

E.PY.C.= Cells of pyloric eminence.

E.ST.= External stipites.

EX.= Exoskeleton.

F.

F.B.= Fat body.

FR.= Frons.

G.

G.= Granules.

G.C.= Gland cells.

G.D.= Gnathochilarial ducts.

G.G.= Gnathochilarial or maxillary glands.

G.P.R.= Proctodeal imaginal ring.

G.S.R.= Stomodeal imaginal ring.

H.

H.L.= Epitheloid layer.

HP.= Hypodermal layer.

HY.= Hypostoma or gnathochilarium

I.

I.= Infundibulum of labyrinth.

I.B.= Interconnecting branches of muscle fibers.

I.C.I.= Inner zone of chitinous intima.

I.L.M.= Inner longitudinal muscles.

I.M.L.= Internal maxillary lamina.

IN.= Intestine.

IN.G.= Intestinal gland.

IN.G.C.= Intestinal gland cells.

I.S.G.= Interstipital groove.

I.ST.= Internal stipites.

IT.C.= Intermediate cells.

L.

L.= Lumen or cavity.

LB.= Labrum.

LE.= Leucocytes.

L.G.C.= Gland cells in advanced stage of secretion.

L.L.= Lobi linguales.

L.M.= Longitudinal muscles.

L.P.= Laminae pectinatae.

M.

M.= Mentum.

M.A.L.= Median anterior lamina.

M.A.T.= Median anterior laminette.

M.C.= Mature cells.

M.E.= External malae of hypostoma.

M.F.= Muscle fiber.

MG.= Midgut.

M.I.= Internal malae of hypostoma.

M.IN.= Middle region of intestine.

M.M.= Mandibular muscles.

M.S.= Possible mitotic figures.

M.ST.= Mandibular stipites.

M.T.= Malpighian tubules.

N.

N.= Nucleus.

N.C.= Nerve cord.

N.D.= Nucleus undergoing chromatolysis.

N.P.M.= New peritrophic membrane in process of formation.

O.

O.C.I.= Outer zone of chitinous intima.

O.L.M.= Outer longitudinal muscles.

O.S.M.= Outer supporting membrane of midgut.

P.

P.= Promentum.

P.CH.= Primary chitin.

P.D.= Posterior dilatations.

P.EP.= Pigmented epithelium.

PH.= Pharynx.

P.IN.= Posterior region of intestine.

P.I.T.= Processus inferior internus tentorii.

P.M.= Peritrophic membrane.

P.M.T.= Proximal rami of Malpighian tubules.

PO.= Pseudocciput.

P.P.T.= Processus posterior tentorii.

PR.= Premandibles.

PR.A.= Premandibular apodemes.

PR.M.= Masticatory plates of premandibles.

PS.= Pores.

PS.C.= Pore canals.

P.S.D.= Posterior salivary ducts.

P.S.G.= Posterior salivary glands.

P.S.T.= Processus superior internus tentorii.

P.T.T.= Pars transversalis tentorii.

P.V.= Pyloric valve.

PX.C.= Prepharyngeal corpus.

PX.L.= Prepharyngeal lateral pieces.

R.

R.= Rugae.

R.C.= Basal remnants of discharged cells.

R.D.L.= Distal ramus of labyrinth.

RE.= Rectum.

7-20 2M

R.G.C.= Regenerative cells.

R.P.L.= Proximal ramus of labyrinth.

R.P.L.C.= Constricted part of proximal ramus of labyrinth with chitinous intima.

R.R.C.= Rectal regenerative center.

S.

S.= Secretion.

SA.= Sacculus.

S.C.= Spiniferous cells.

S.CH.= Secondary chitin.

S.G.= Secretory granules of midintestinal epithelium.

SE.P.= Sensory pits.

SK.M.= Skeletal muscles.

SP.= Spatula.

SP.C.= Cardiac sphincter.

SP.P.= Pyloric sphincter.

SP.R.= Posterior intestinal sphincter.

SS.= Spines.

S.T.= Supporting tissue.

T.

T.= Testes.

T.G.= Tubular gland.

TR.= Tracheae.

TRL.= Intracellular trachecles.

TR.C.= Tracheal end cells.

TR.P.= Peritracheal cells.

V.

V.= Ventrad.

V.B.B.= Vestigial brush border.

Note.- In all compound abbreviations the elements separated by hyphens must be referred to individually.

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II. MATERIAL AND METHODS

The species which I have investigated are, Parajulus, venustus (Wood), Scytonotus granulatus (Say), Orthomorpha gracilis (Koch) and Fontaria virginiensis brunnea (Koch). All except Orthomorpha were recorded as occurring in Minnesota by Bollman (1893), the only Diplopodologist who has collected in this state. But in identifying the species I found it inadvisable to depend on Bollman's keys which are now out of date in many respects, and consequently enlisted the aid of Dr. R. V. Chamberlain of Harvard who generously made the determinations for me.

All of my Parajulus material, which comprised over three hundred specimens including adults of both sexes and immature in all stages from the 14 mm. upward, I collected in the late summer and early fall of 1919 from one small locality. My Orthomorpha material consisted of about fifty male and female adults and a similar number of sixth and seventh instar immature which were taken from a greenhouse in late November. The specimens of both Scytonotus and Fontaria, which numbered only twenty in each instance, were obtained in the early fall from the same locality and comprised both sexes but no very young individuals.

I wintered about one hundred and eighty of my Parajuli in goldfish globes six inches in diameter which contained moist loam to a depth of three inches and were provided with mosquito netting covers. From thirty to forty specimens I assigned to each globe, kept the mosquito netting constantly moist and never

exposed the globes to direct sunlight. As food, I supplied pieces of decayed apple, banana, dead leaves and roots which I promptly replaced whenever I saw indications of mould or possible Nematode or Acarine parasites. In this way I maintained what were apparently normal conditions, since the specimens remained active and fed regularly throughout September and October and experienced very few deaths. I failed, however, to observe any indications of ecdysis on the part of either the young or mature individuals. Later, with a view toward offsetting the possible ill effects of dry air and varying room temperatures, I kept the globes securely wrapped in wet, coarse towels. This reduced the light and heat within the globes sufficiently to induce hibernation. Thereafter I was unable to get any of my specimens to become active and feed until they had been exposed for at least five minutes to sunlight and warm room temperature. From that time on until the middle of February, 1920, when I disposed of the remainder of my living material, the percentage of deaths rose steadily but never reached high proportions.

For wintering the other genera I employed methods similar to those just described and met with equal success. In all, I kept about one hundred Orthomorphae, five Scytonoti and five Fontariae and, in the case of the last two, which are genera that subsist largely on decayed ligneous matter, I substituted decayed bark and wood for softer plant tissue. Occasionally I was able to induce Scytonotus to feed on apple and banana but had no success with Fontaria in this regard. The Orthomorpha

specimens, however, fed as readily on decayed cellulose matter as Parajulus and also showed a fondness for fresh lettuce leaves. Unlike the other genera, they evinced only a slight tendency toward hibernation during the winter months, though subjected to the same conditions. Upon examining them, I always found some individuals feeding while most of others readily followed suit after a few minutes exposure to warm air and sunlight. This would suggest the possibility that through adaptation to an artificial hibernal environment (a phenomenon which is by no means peculiar to this species of Diplopod) Orthomorpha is gradually losing its habit of hibernation.

All of the Diplopod material, which I reserved for ordinary histological examination, was killed and fixed during the months of August, September and October when the specimens were most active. The bulk of my dissections were made during both fall and winter, but my starvation experiments, together with the killing, fixing and dissection of the specimens concerned, were confined to late fall and winter.

Dissection for the purpose of studying the interrelationships of the internal organs is a procedure especially difficult in Diplopods, because of the brittleness and rigidity of the body rings and the relative ease with which the segments may be detached as compared with more heteronomous, short bodied Arthropods. Plateau (1878), who is apparently the only one that has suggested special methods of dissection, advocates making a middorsal and a midventral incision the entire length of the animal and then placing the specimen on a piece of dry cork

and carefully separating the two halves. I have found this method not only very hard to perform successfully but also totally unsuited for determining the relationships between the various regions of the digestive tract and the segments of the trunk. After many futile attempts in one direction or another, I finally devised a procedure which, though not as simple and time saving as I could wish, always gave satisfactory results. In the first place, I etherized the specimen to be dissected until it became inactive but was still relaxed. Then I poured melted paraffin into a mold and, while allowing time for it to cool and harden at the bottom and sides of the latter, I gently rolled the specimen on a smooth surface until its body was reasonably straight and rigid. I next placed it, dorsal side up, in the central part of the mold where the paraffin was still melted but too cool to have any damaging effects on the body tissues. Finally, I quickly hardened the paraffin by immersion in cold water and was thus able to shave off the exoskeleton from the entire dorsal surface of the animal which was now securely held in place by the paraffin. By heating the base of the paraffin block and adhering it to the paraffin bottom of a dissecting pan, I was able to keep the specimen well submerged in a distilled water, salt or alcohol solution and therefore minimized the chances of its becoming detached and rising to the surface of the liquid in the course of further dissection.

When the digestive tract alone was required for gross or histological study, I found that a few simple manipulations were all that was needed for removing it in good condition. I first

allowed a specimen to crawl over a smooth, hard surface, preferably a table top and with two clean, quick razor strokes dissevered the head and anal segment. Then I picked up the specimen and by twisting one end of the trunk in one direction and the other in the opposite, caused a severance of the body rings at approximately the middle point and, at the same time, freed the digestive tract from its tracheal and connective tissue attachments to the body wall. The final step consisted in gently pulling the two halves of the trunk away from each other and allowing the freed digestive tract to slip out between them. In this way I was able to secure the entire alimentary system with the exception of the pharynx, rectum and some of the distal coils of the Malpighian tubules. I have described this simple operation in detail merely to emphasize the importance of twisting the two halves of the trunk before pulling them apart, since, otherwise, a more or less abnormal extension of the tract, particularly the midgut, is caused.

For most of my histological material, I used Bouin's picroformol and Flemming's fluid as fixatives and had essentially the same experience which many others have met with in the use of these reagents. Because of its permeating qualities, which I often increased by adding a few uric acid crystals, I found Bouin's fluid most satisfactory and by far the most dependable, especially for sections through the head where there is a great deal of chitin and a number of large tracheae. On the other hand, Flemming's fluid served best in bringing out specific cytological distinctions between early and late stages in the

cycle of various secretory cells such as the epithelium of the midgut. For a few midguts of Parajulus and Orthomorpha, I used Hermann's fluid but could detect no reactive difference between it and Flemming's solution.

I embedded all of my material in hard paraffin which, where the tissue was well fixed and infiltrated, proved satisfactory except for some of my largest blocks. Inasmuch as the contents of the digestive tube always includes pebbles of various sizes and pieces of wood in Fontaria and Scytonotus, I depended on the easily replaceable Gillette razor blades for most of my sectioning. By allowing only one or two millimeters of the cutting edge of the latter to project beyond the clamps, I was able to reduce the vibrations of the blades to a minimum.

As regards the staining methods employed, I have little of special importance to note at this point. For general staining, haemalum, haemalun-eosin, haemalun-eosin Orange G. and especially Mallory's connective tissue stain proved efficacious in combination with Bouin's fixation, but could not always be relied upon with Flemming's fluid, probably because of too great an interval of time between fixing and staining. On the other hand, Benda's iron haematoxylin and acid thionin almost invariably worked well with Flemming's, particular in further intensifying structures already brought out by the fixation.

III. SUMMARY OF THE LITERATURE.

As far as my present knowledge goes, the literature on the digestive tract of Diplopods is rather meagre, in as much as the majority of the works treat the subject either very briefly or incidentally in conjunction with general accounts of the internal structure.

Apparently Ramdohr in his "Abhandlung über die Verdauungswerkzeuge der Insecten"(1811), was the pioneer in this field of investigation, since he presented a gross figure of the digestive tube of Julus terrestris (Linn.). Later in 1817, Treviranus showed a somewhat similar figure of the same species in "Vermischte Schriften". Then followed the "Beiträge zur Kenntnis des innern Baues von Glomeris marginata" of Brandt, in 1837 in which the gross structure of the digestive tract and tubular (anterior) glands was figured and described. Shortly afterwards in 1841, Brandt published a second work, "Observations sur le genre de la vie et la physiologie des espêces du genre, Glomeris", wherein he notes the habits of the female Glomeris in enveloping her eggs with earth from her hind - intestine. In 1847, Rymer Jones showed a figure of Julus terrestris in his "Cyclopedia of Anatomy", which was based largely on the drawing of Treviranus. The next contribution was made by Leydig, who figured and described the Malpighian tubules of Julus terrestris in his "Traite d'histologie de l'homme e des animaux" of 1866. Like Ramdohr he showed them as four in number, but he was the first to figure the epithelium which he accurately represents as being composed of small light yellow cells. After Leydig came Bode, who gives us a precise though limited gross description of the digestive tract of Polyxenus lagurus (De Geer) in "Ein Beitrag zur Anatomie,